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SOME DYNAMICS OF LEAF VARIATION IN *ASCLEPIAS TUBEROSA*

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I. INTRODUCTION

One day many years ago, as a young student, I paid my first visit to the Smithsonian Institution in Washington. When noontime arrived, I was taken in tow by my new friend, E. P. Killip, to the Smithsonian's unofficial "Lunch Mess" in the kitchen of an old house around the corner. There I was awed by my inclusion within a jovial group of biologists previously known to me only by their eminence. Killip announced me as a budding authority on the Asclepiadales, an order of Flowering Plants including the milkweed genus, *Asclepias*. Instantly the late Dr. F. V. Coville fixed me with a baleful glare and thundered: "All right, then tell us what is wrong with *Asclepias tuberosa!*" I was dumb-struck. I knew *A. tuberosa* in the field about my home in St. Louis, but it had never occurred to me that anything was "wrong" with it; and besides, I was having troubles of my own with my dissertation topic, the exasperating genus *Apocynum*.

At any rate, when my taxonomic studies finally brought me to *Asclepias* shortly before the outbreak of the recent World War, I already was prepared to find something "wrong" with *A. tuberosa*. And I did. The species, as is usual in the genus, is beautifully distinguished by sharply defined floral and vegetative characters; it is easily keyed from its congeners. But within the species extraordinary variation is rampant, particularly in the leaves. By overworking my taxonomic intuition, at length I was able to distinguish three subspecies, which went far toward resolving the difficulty. But I could not escape the knowledge that something still was "wrong," particularly at the peripheries and commissures of the subspecific distributions. Nevertheless, but for the outbreak of the war I probably would have been content to let well enough suffice.

Every taxonomist is all too familiar with the professional handicaps imposed by a world conflict. Even for those who fortunately are left at home, special duties demand attention. Furthermore, necessary facilities for research are cur-

tailed, such as the exchange of authentic or type specimens. Nor can one overlook the difficulties of publication itself, thanks to wartime industrial disturbances. Anticipating this prospect, I decided to take advantage of international catastrophe by familiarizing myself with some of the more recent tools of biological systematics to the end of applying them to the special problems presented by *Asclepias tuberosa*.

II. Biology of the Species

Asclepias tuberosa is familiar to practically any one who is interested in wild flowers from Sonora to Massachusetts and from Minnesota to Florida. Throughout approximately the eastern half of the United States it is a common roadside plant, conspicuous to any passer-by because of its clusters of stems about knee-high, each surmouted in midsummer by showy trusses of smallish but intensely brilliant orange, scarlet, or yellow flowers. The plants are long-lived perennials of easy culture, and are prized by many horticulturists because of their dependability, long season of bloom, and dramatic dashes of color.

Not the least interesting feature of the flowers is their apparently irresistible appeal to insects, particularly Hymenoptera, which are their chief pollinating agents. Butterflies, as well, are almost constantly hovering above blooming plants, and are responsible for their most familiar popular name of butterflyweed. Coralweed also is an appropriate name for them. Fortunately less familiar are the names pleurisyroot and chiggerweed.

VEGETATIVE HABIT

A fully developed butterflyweed usually is a rather massive plant. The perennial portion consists of a woody tap root as much as three feet long and eight inches in circumference, surmounted just below ground level by a tightly branching crown from which a few to as many as a hundred herbaceous flowering stems may arise each year. Plants attain blooming age two to three years after germination of the seed and may persist for as long as twenty years or more. It would be difficult to estimate the age of a large plant upon a single examination because of the numerous stems produced each season and their crowding at the crown.

Some botanists would refer to the perennial plant body which has just been described as a "clon," and the term has been applied to the essentially similar structure in the Viorna section of *Clematis* (Erickson, 1945). It should be borne in mind that in butterflyweeds, as in other similar plants, the communities of clustered stems have no greater degree of individuality than have the separate twigs of a tree. They are connected organically to the same tap root, and are ramifications of a single embryonic plumule. In butterflyweeds there are no vegetatively reproducing stolons, rhizomes, gemmiferous roots, nor other special propagulae. It is conceivable that accidental or purposeful operation might result in the successful division of the crown into two or more parts, although I have not been successful in the attempt. But such division in nature, if it occurs at all,

must be contrary to the habit of the species, since I have observed no instance amongst the several thousand living plants which I have examined.

It so happens that in certain other species of *Asclepias*, as in the common *A. syriaca*, adventitious buds upon special gemmiferous roots habitually succeed in multiplying single plants. These compose true clons such as those of *Hemerocallis*, *Iris*, *Robinia*, and other spontaneously vegetative-propagating plants. To call the plant of butterflyweed a clon in my opinion not only is misleading but destroys the contrast of the vegetative propagation of such a species as *A. syriaca*. It is difficult to imagine a plant which under some unusual circumstance might not become divided into two or more. If a term is allowed to become a quibble, its significance is lost.

The herbaceous stems of butterflyweed range approximately from one to three feet in height. They normally are unbranched save at the terminal region of inflorescence, although occasional axillary branches may be encountered most frequently as the traumatic result of early decapitation. It must be emphasized at this point that the herbaceous stems are produced at one time at the beginning of each season, and are of essentially identical age. They are remarkably similar in height and rate of development, as well as in number and relative size of parts. These factors are of obvious advantage in the random collection of leaves for statistical analysis.

The stems of butterflyweed are determinate, ending in an umbelliform cyme of approximately one to two dozen pedicellate flowers. In most fully developed plants the terminal cyme is subtended by two or more leafy-bracted, scorpioid branches studded at the nodes with umbelliform cymules developing in acropetal succession. These branches obviously are the homologues of the branches of a dichasium. The determinate inflorescence character of *A. tuberosa* is an anomaly amongst the American species of *Asclepias*. It is an extremely fortunate one from the standpoint of these investigations, since it further facilitates the collection of leaves of nearly identical physiological age, which would be a precarious operation upon an indeterminate axis.

The leaves are simple, entire, and are irregularly alternate or spirally arranged. The number, shape, and size of leaves are extremely important characters in the distinction of the subspecies, and will be discussed in later paragraphs of this section. Obviously, the leaf variability is such that it forms the subject matter for these investigations.

REPRODUCTIVE HABIT

The flowers of *Asclepias* are classical examples of entomophily and are equalled in complexity only by those of the orchids. In the present connection it will probably suffice to recall only those features immediately concerning pollination and the production of seed. In the center of a butterflyweed flower, as in other milkweeds, there arise five cornucopia-shaped bodies which are petalaceous, and are in fact often mistaken for the corolla. These are the *hoods*, the nectar-secreting

bodies which are the goal of the insect visitors. The hoods actually are outgrowths of the staminal filaments, the smaller anthers of which they virtually conceal.

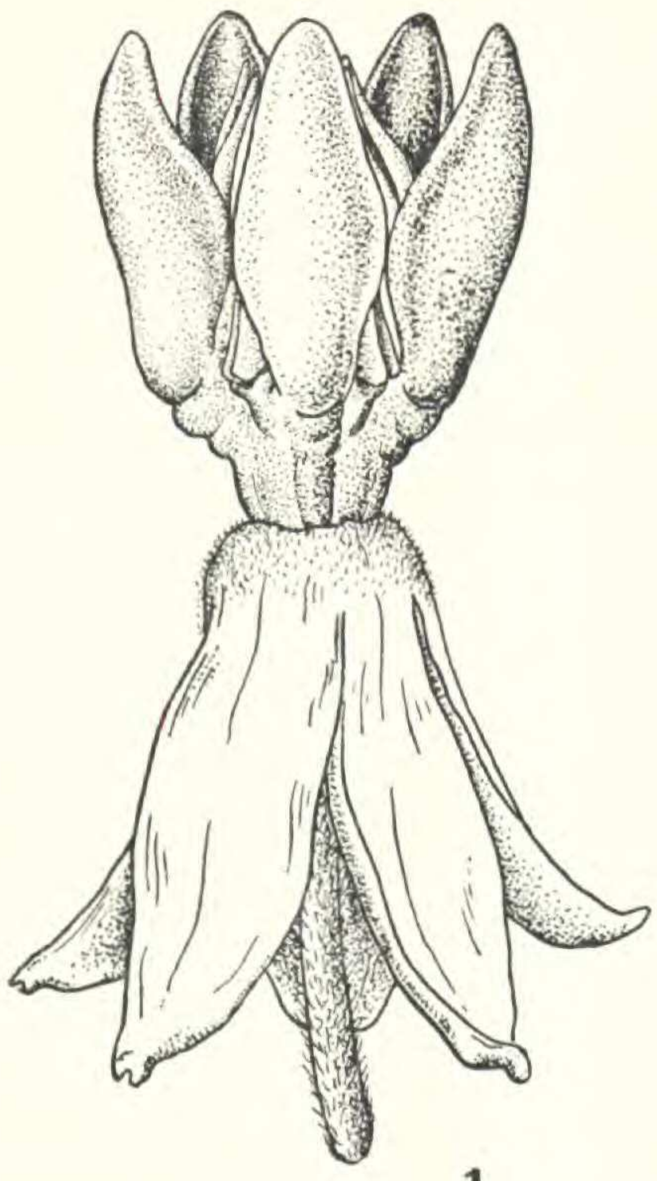
The anthers themselves are closely connivent in the form of a cylinder or truncated cone about the stigma. Each anther contains two pollen cavities. A remarkable feature of milkweed pollen is that it is borne within small, flat bags, or *pollinia,* the confining membrane being derived from the tapetum. Still more remarkable is the fact that the pollinia of adjacent anthers are joined together in pairs by means of a delicate yoke-apparatus *(translator)* surmounted by a pad-lock-shaped body known as the *corpusculum.*

The corpusculum bears upon its outer face a more or less conspicuous cleft. It is well known that pollination is initiated when a strong insect, such as a wasp, accidentally thrusts its barbed legs between the anthers while scrambling about the center of the flower in search of nectar. If a barb of the insect's leg wedges into the cleft of the corpusculum, a stout pull of the member usually succeeds in withdrawing the pair of pollinia from the anthers. It is a common sight to see wasps or bees flying about a blooming butterflyweed, their legs laden with pollinia.

Robertson (1892) has enumerated 15 species of Lepidoptera, Hymenoptera, and Diptera collected while bearing on their bodies pollinia of *Asclepias tuberosa* in the neighborhood of Carlinville, Illinois. Amongst these is *Apis mellifera,* the common honey bee, which is known to have a flight radius of one-half rarely to five miles. It is difficult to secure data concerning the radius of flight of the other possible pollinators, although the phenomenal migrations, some hundreds of miles, of certain Lepidoptera are well known.

I do not wish to over-emphasize the efficacy of the floral mechanism of *Asclepias* with regard to insect visits, since it does not appear to be very high. Certainly less than 1 per cent of the flowers normally set fruit, except in *A. incarnata,* the swamp milkweed, in which sets may amount to 25 per cent. An additional factor to recall, in connection with insects as pollinators of *Asclepias,* is that the pollinia appear to be highly irritating to the carrier. On several occasions I have trapped wasps of the genus *Chlorion* in transparent bags, when they invariably appear to be more anxious to divest themselves of the pollinia than to escape.

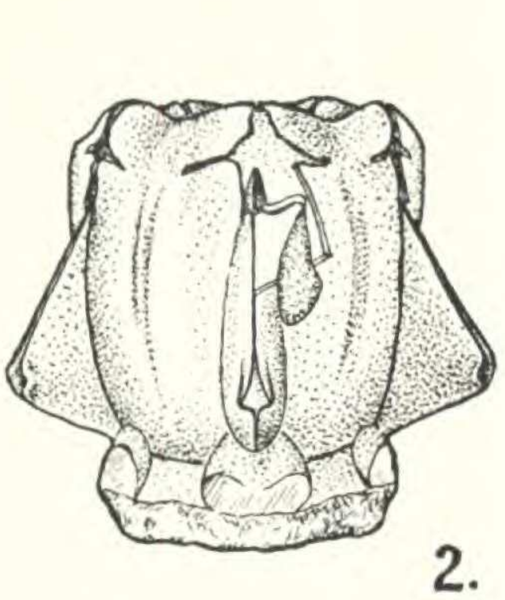
The stigma of the milkweed flower is surrounded by the connivent anthers and is a rather complex structure. The receptive surface is not at the flat top, but actually is divided into five concave surfaces which alternate with the anthers and are closely protected by them. In order that a stigmatic surface be pollinated, it is necessary to introduce a pollinium between the flanged, cartilaginous, marginal wings of the anthers, an extremely delicate and nerve-wracking operation for a human experimenter. That the feat is accomplished at all by the chance movements of an insect seems nothing short of marvellous, and that so few fruits usually are observed upon a single plant is quite understandable.



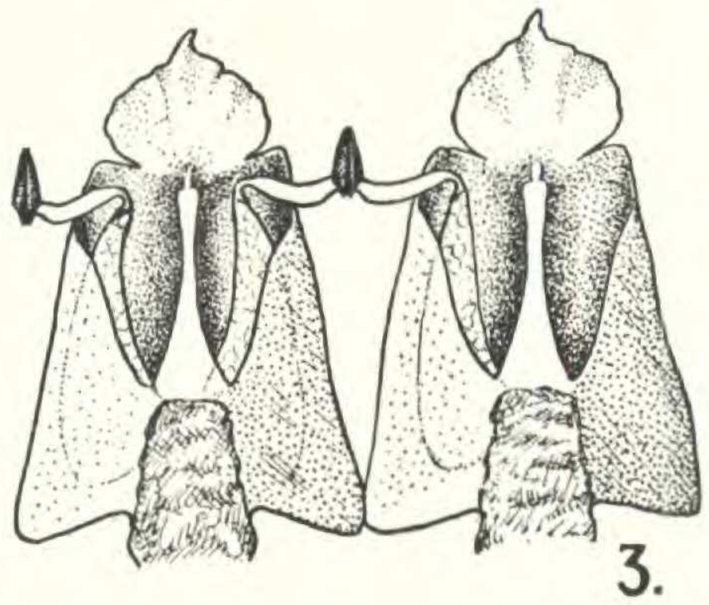
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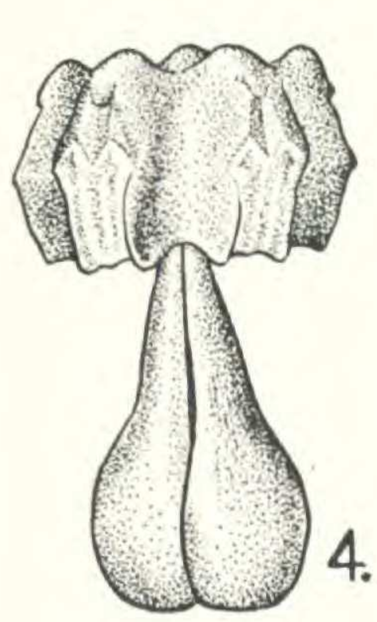
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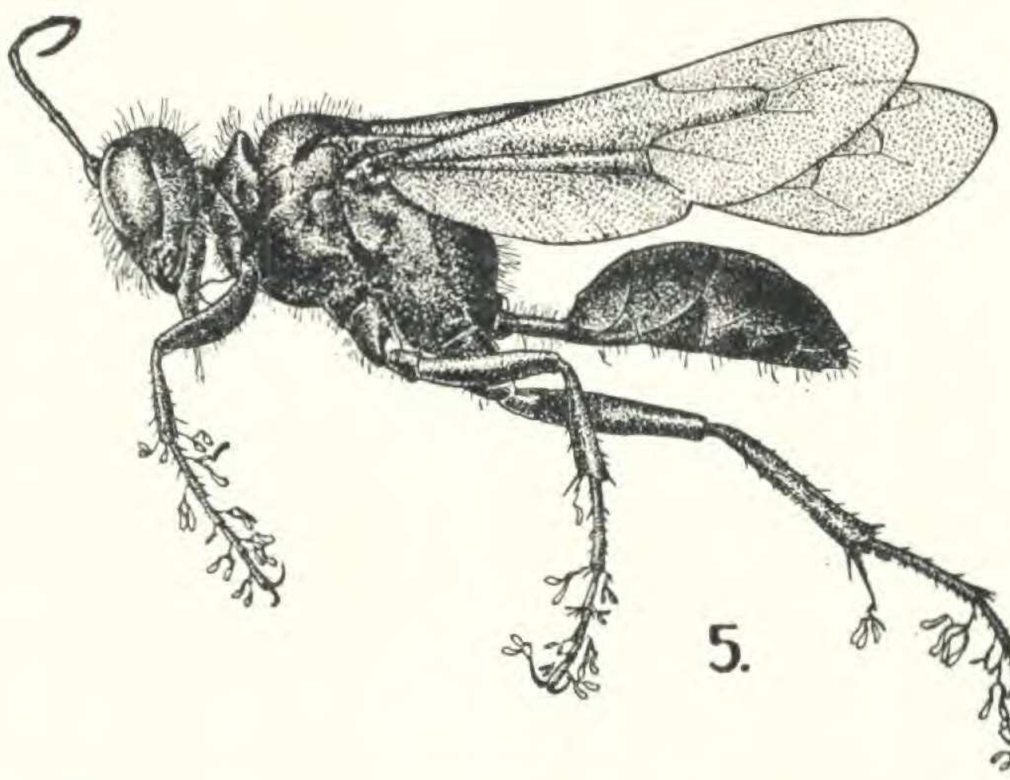
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6.

E. Herbold Froeschner

Reproductive mechanism of *Asclepias tuberosa:* 1, flower; 2, gynostegium with hoods removed, showing connivent anthers with one pollinium protruding; 3, two anthers as seen from within, showing pollinia; 4, carpels with stigma head, showing two stigmatic surfaces; 5, *Chlorion* sp. bearing pollinia on feet; 6, pollinia enlarged, attached to barb of insect's foot; 7, follicles with comose seeds.

Size and shape of pollinia, corpuscula, anther wings, and stigmatic chambers vary greatly amongst the species of *Asclepias*. Hense it is not surprising that interspecific hybridization within the genus is very infrequent. After over a decade spent in studying it, I doubt whether I have observed many more than a dozen instances of putative hybrids amongst the approximately 80 species.

The only record of a successful experimental cross between distinct species is that of *A. speciosa* × *syriaca*, first performed by Stevens (1945). In crosses involving other species, Moore (1946a) occasionally observed preliminary swelling of the ovary, followed by abortion. This he interprets as due to somatoplastic sterility. Although successful self-pollinations have been reported by several authors for certain species of *Asclepias* (notably Stevens, 1945), similar experiments by Moore (1946b) were unsuccessful. My friend F. K. Sparrow has told me that his extensive pollinations with *A. syriaca* reveal clonal self-sterility. My

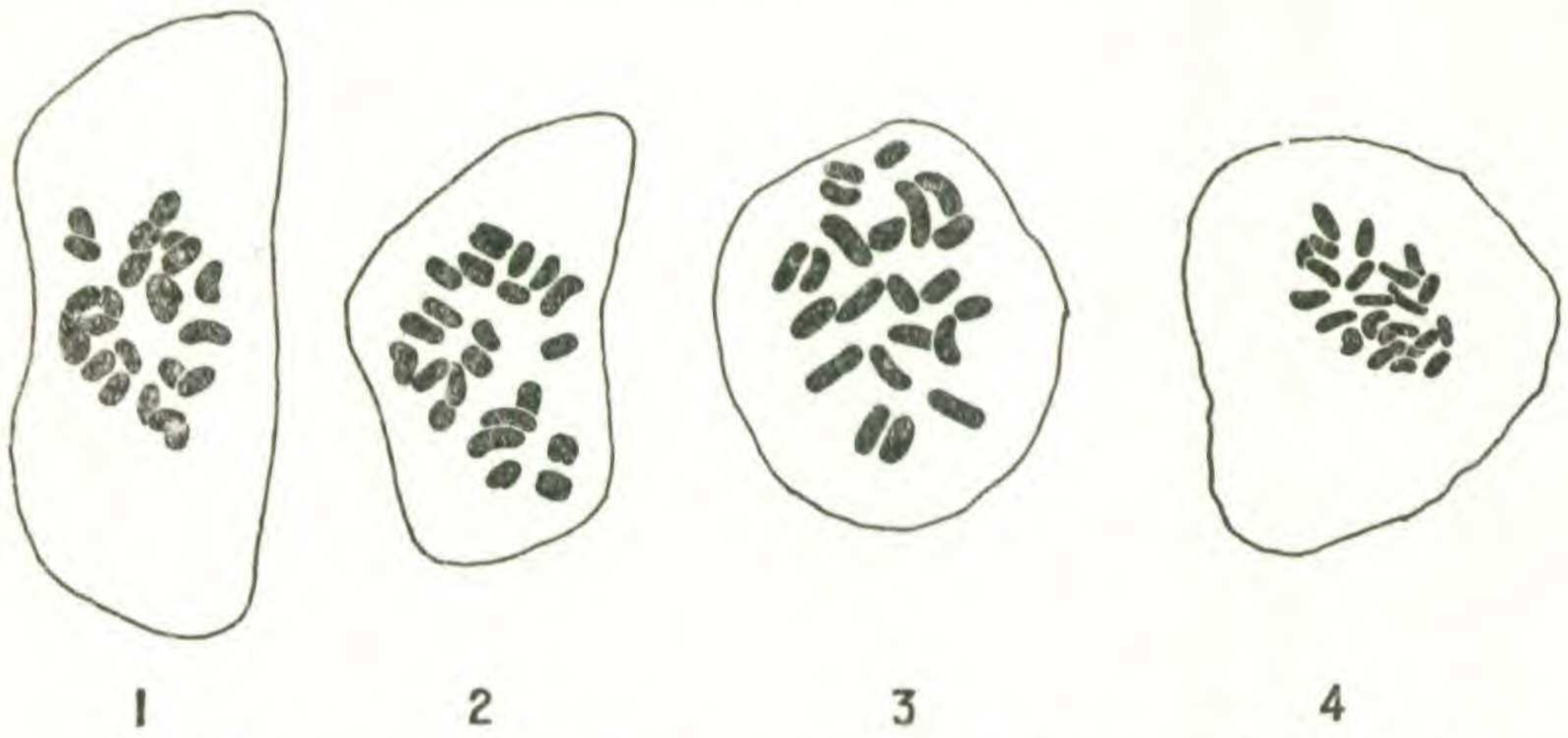


Fig. 1. Somatic metaphases from young leaves of *Asclepias tuberosa* in different parts of its distribution: 1, Stillwater, Okla.; 2, Glendale, Mo.; 3, Westport, Conn.; 4, Snail Lake, Minn.—All figures × 1500.

own limited experiments at self- and cross-pollinations involving *A. tuberosa* have been notably futile. I suspect that special mechanical factors may account for the difficulty in milkweed pollinations, such as the degree of desiccation of the tapetal membrane, which must split to allow the emission of the pollen tubes.

The fruit of butterflyweed consists of solitary, or infrequently paired, narrow, fusiform follicles up to 15 cm. in length. Upon dehiscence as many as 100 compressed, oval seeds approximately 0.4 cm. long are released, each provided with the micropylar parachute of silky hairs so diligently studied and collected as a substitute for kapok during the recent war. The silky parachute, technically called the *coma*, is extremely bouyant, and is doubtless capable of conveying the attached seeds for long distances, even approximate estimates of which, however, are unavailable.

I have found during the course of progeny tests that viability of the seeds is fairly high as a rule, but that germination is very irregular, proceeding in some samples for well over a month. Although I am not yet ready to publish con-

clusions upon these tests, they indicate at the present writing that the various leaf modifications encountered in different parts of the species' distribution have a genetic basis and are maintained within sufficient limits under cultivation in my test plots.

CYTOGENETICS

Chromosome counts for *Asclepias tuberosa* made by various workers, notably Moore (1946), agree in the figure $n = 11$. This is also the base number for all other Asclepiadaceae investigated. Polyploidy has not been reported in *Asclepias*, although tetraploids occur in certain other genera, particularly in the Orient. Somatic metaphases from young leaves of *A. tuberosa* in various parts of its range are reproduced in fig. 1. The chromosomes are small (about 2 μ long) and relatively uniform, and are poor subjects for configuration or structural studies.

ECOLOGY

In its geographical distribution from southern peninsular Florida to northern Sonora and from the Ottawa River to the Black Hills of South Dakota, *Asclepias tuberosa* demonstrates its wide climatic adaptability (Map I). It is clear from the map, as well as substantiated by my field observations, that the species is best adjusted to its environment in the mesothermal and southern microthermal climatic regions of North America. Where it is found in the western steppe climates it is probably as a scattered relic of former mesophytic times.

Something of the climatic preferences of butterflyweed can be deduced from a comparison of the distribution map of the species with standard climatic charts of North America. At least in general outline, it appears that the July mean temperature is critical in relation to density of population of the plants, a normal mean surface temperature of 68° to 86° F. indicating roughly the optimal limits. Precipitation appears to be more critical than temperature, however, suggesting general requirements of an annual mean of over 20 inches. It is very striking, when traveling eastward across Kansas in midsummer, to find the butterflyweed suddenly emerge from more sheltered positions as a common roadside plant on the outskirts of Topeka, near the boundary of the tall-grass prairies and the short-grass plains.

In the opinion of some, *Asclepias tuberosa* should be considered as a prairie type, or even as an emigrant from the dry plains or deserts of northern Mexico. To my mind it accords more closely with the facts of distribution to regard it as indigenous to the glades and open woodlands of the southern hardwood forests, from which it has spread to the southeastern longleaf, loblolly, and slash pine forests, and to the southwestern pinyon-juniper-yellow pine woodlands. When one considers that approximately the northeastern third of the species' present distribution has been available for plant colonization only since the Pleistocene, it is clear that establishment of populations is taking place to the northeast much more rapidly than to the southwest.

Butterflyweed is found at elevations from near sea-level to about 6000 feet altitude. In the western states progressive desiccation of the plains appears virtually upon the point of eliminating the species except upon the well-watered highlands. In the plains the plant must seek the protection of ravines and canyons, or larger neighboring plants.

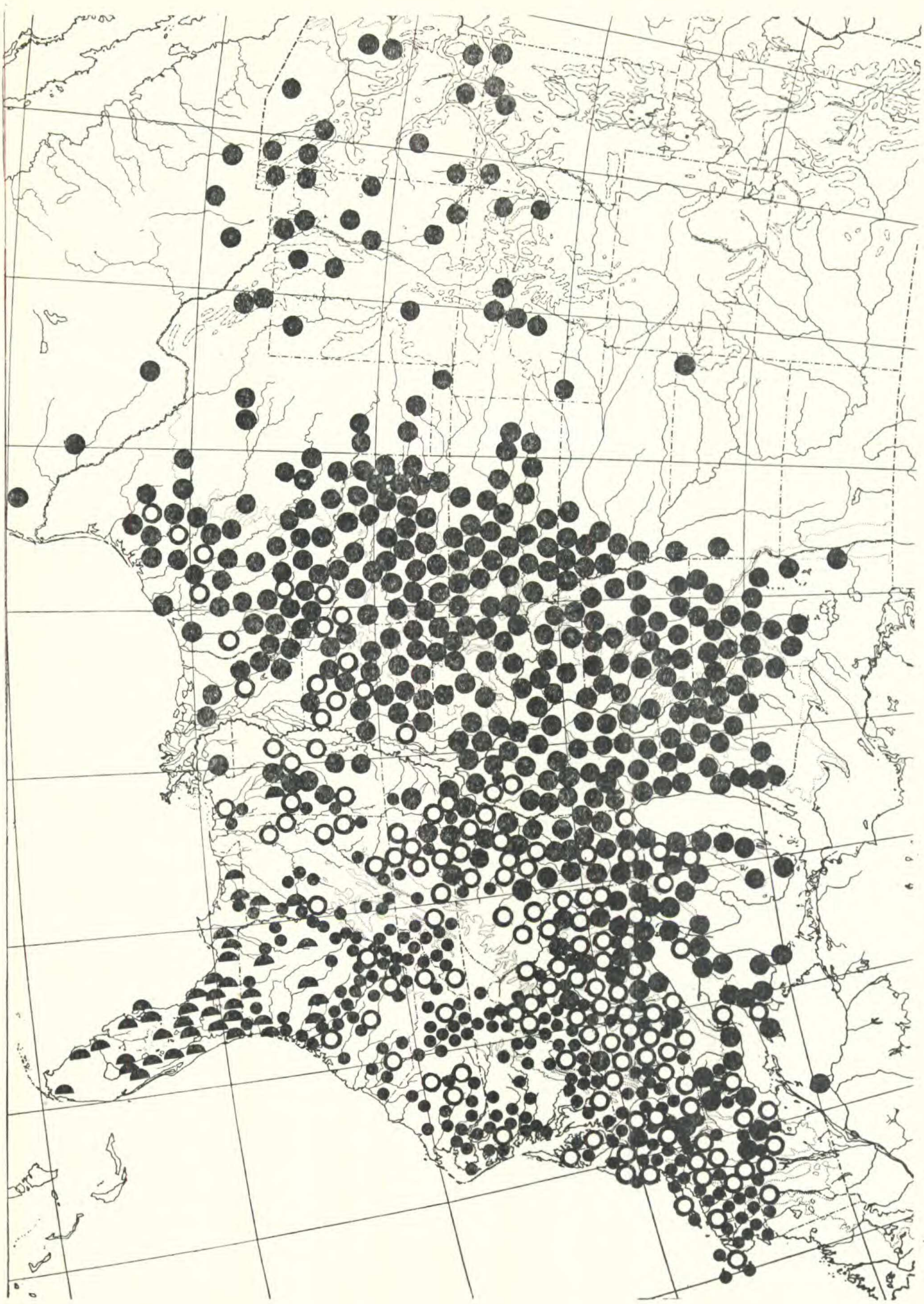
The wide distribution of *A. tuberosa* bespeaks its tolerance for a broad range of edaphic conditions. Horticulturists are in the habit of prescribing for it a sandy soil, upon which it undoubtedly flourishes, but scarcely more so than upon the exceptionally tight clays known as "crawfish soil." Although I have made no attempt to determine its pH preferences, they probably are circumneutral since I have found fine colonies of plants growing impartially upon dolomitic limestone, argillaceous shale, and granitic detritis. An unusually large colony was found on an alkaline flat in western Texas, but the plants appeared depauperate. Good soil drainage appears essential for optimal growth, and a "poor" soil is generally preferable to a "rich" one. I do not remember ever having found it growing on alluvium.

Butterflyweed is found occasionally as single plants, but more frequently in colonies of three or four to well over a hundred individuals. Distance between colonies varies notably with respect to local climatic and vegetational conditions. Roughly east of the 96th meridian the species is a common roadside plant, as has been discussed before. Through eastern Kansas and Missouri the colonies may be encountered at intervals averaging about ten miles apart.

Through the prairies of south-central Illinois, on the other hand, I was able to find only three colonies along the route of about 150 miles between St. Louis and the Wabash River. From southern Indiana to West Virginia the colonies become somewhat more frequent, and reach their greatest frequency, somewhat more than in Missouri, from West Virginia to the coast of Virginia. The brief account of this transect summarizes observations made during a collecting trip in the summer of 1946. Statistical details will be presented in a subsequent chapter.

Roughly west of the 96th meridian butterflyweed is scarcely ever encountered along roadsides through the Great Plains. The plants are found, if at all, only along the infrequent water courses, particularly at the heads of ravines. The size of colonies is considerably smaller than is customary in the East, and the distances between them is far greater. It is only in the pinyon-juniper-yellow pine highlands of the southwestern states that butterflyweed again becomes a fairly frequent plant.

I believe that colonies usually develop from seedlings of a single parent plant. This is indicated not only by their considerable degree of isolation, but by the centering of leaf variation amongst individual plants about more or less distinctive colonial means for the various characters measured.



Map I. Distribution of *Asclepias tuberosa*: each symbol represents a single county record. Large dots: *A. t. interior*; small dots: *A. t. tuberosa*; hollow circles: putative hybrids *A. t. tuberosa* × *interior*; half-circles: *A. t. Rolfsii*.

THE THREE SUBSPECIES

Ordinary herbarium methods disclosed at the outset of these investigations the presence of three subspecies of *Asclepias tuberosa* (Woodson, 1944): *A. t. tuberosa*, with leaves typically obovate to linear-oblanceolate, the base usually cuneate or rounded; *A. t. interior*, with leaves typically ovate to ovate-lanceolate, usually with cordate or truncate base; and *A. t. Rolfsii*, with leaves essentially as in ssp. *tuberosa* but predominantly with more or less conspicuous hastate or cordate dilation toward the base and with the margins more or less crisped. Map I shows the known distribution of the three subspecies and indicates the probability that the centers of modern dispersal, if not of actual origin, may be regarded as the Paleozoic land masses Appalachia and Ozarkia, and the early Mezozoic "Orange Island," now north-central Florida, respectively.

It is difficult to indicate with such a map the variation and intergradation of taxonomic units, since in this case only three types of symbol are employed. In addition to the symbols for the separate subspecies, however, a fourth, the hollow circle, has been introduced to indicate intergradations of *A. t. tuberosa* and *A. t. interior*. A fifth type of symbol might further be used to show intergradation of *A. t. Rolfsii*, particularly with ssp. *tuberosa*, since as it stands the map rather implies that *Rolfsii* is genetically more isolated than the other two subspecies.

As a matter of fact, such is far from being true. The distribution of hollow circles suggests that in southern Alabama and southern Georgia one might expect to find intergradations of all three subspecies. This actually appears to be the case, and the practical limits of such a map stand revealed. A fifth symbol is not used for intergradations of *Rolfsii* simply because I cannot distinguish the separate roles of the three subspecies satisfactorily.

Almost the first glance at Map I will show that although ssp. *tuberosa*, indicated by small dots, is distributed roughly from the western Appalachian foreland to the coast, with *interior*, indicated by large dots, to the west and north, the hollow circles, which indicate subspecific intergrades, extend from the commissure of the subspecies completely through the distribution of ssp. *tuberosa*. It is clear even from routine examination of herbarium specimens that *tuberosa*, situated unstrategically between *interior* and the sea, is in the process of genetic dissolution.

This situation appeared so interesting that a biometric study of natural and artificial populations of *A. tuberosa* was begun early in 1942. Begun as a side-line to my more orthodox systematic studies, my hobby soon grew to occupy the majority of my research. So many additional topics of interest arise as time passes, and so many new lines of attack suggest themselves, that the study might possibly be continued as long, if scarcely so profitably, as the classic investigations of Sumner on *Peromyscus*.

III. Exploratory Methods

The disadvantages of the type of distribution map which has just been presented in the previous chapter are the simple consequence of the use of a discontinuous scale with too few intervals. Nevertheless I do not wish to minimize its use. In dealing with a genus of many species, such as *Asclepias*, it is ordinarily the only type practicable. It at least states the known range of one or more taxonomic units and perhaps suggests the region of any intergradation. To an imaginative mind one of its virtues may be that it asks more questions than it answers.

When a continuous scale is available, however, measurements of a large series of specimens may allow the accumulation of equally spaced means and their accompanying measures of variability, and the result is a "phenocontour map" such as that advocated by Huxley (1938). As yet few phenocontour maps have been published. Possibly the most familiar examples are those of Alpatov (1929) for *Apis mellifera*, the common honey bee, in European Russia. These, in my opinion, suffer chiefly because of the relatively few and irregularly distributed localities into which the many samples fall. A better instance is provided by Pearson's (1938) geographic study of melanism in the Tasmanian bush opossum, *Trichosurus vulpecula fuliginosus*, in which definite contour lines ("isophenes") were obtained. In a class by itself is the world chart of human blood groups presented by Boyd (1939).

From a phenocontour map benefits may accrue from several directions. The biogeographer may plot with a degree of mathematical precision the migrations and environmental adjustments of which he now speaks in more general terms. The cytogeneticist may be given wholesale data of population dynamics upon which to apply a gamut of attractive theory much of which still requires exemplification. Last, but not least, opportunity finally is given the customarily inarticulate systematist to prove the detail of his observations to a disbelieving world. The inexorable accumulation of specimens to catalogue for the benefit of others may allow but one such opportunity, and it should be taken.

USE OF THE HERBARIUM FOR POPULATION STUDIES

There can be little doubt that systematic botany has contributed far less to recent advances in the study of evolution than has systematic zoology, and one reason for this has been its neglect of modern statistical methods. Yet for ready collection of data, ease of manipulation, and wealth of museum material, plants in general are much more favorable subjects for study than are animals. No one has appreciated these advantages more than did Charles Darwin, who bequeathed a part of his estate for the founding of the 'Index Kewensis,' the herbarium taxonomist's most indispensable single tool.

Herbarium specimens are not a perfect substitute for living plants, but they offer incalculable advantages for the interpretation of field studies. Not all plant materials are adequately preserved by the usual herbarium methods of press-

ing and drying, but an astonishing percentage is. In the herbarium of the Missouri Botanical Garden is a collection of several hundred dried plants assembled by one Georg Rudolph Boehmer as material for his 'Florae Lipsiae Indigena,' published in 1750. The appearance of some of these plants is almost as though they had been pressed and dried but a few months ago. All are perfectly recognizable, and we have in them a detailed record of the distribution of plants around Leipsic two centuries ago.

In the early days of botany it was customary to have represented in the herbarium only one or two specimens of each species. Nowadays any of the several major herbaria of the world may include a thousand specimens of a single widespread species from all parts of its range, gathered in all stages of its growth at all times of year by faithful collectors, living and dead, for at least a century. When several such collections of a group of plants are united for one's study, the very mass of it is most impressive. The accumulation of material so representative of variation in time and space obviously is beyond the powers of an individual. It is a unique evolutionary heritage.

A false impression widely current among non-taxonomists is to the effect that herbarium specimens usually are collected because of some abnormality which attracts the fancy of the collector. The accusation reveals such prejudice that one is baffled for an effective retort. Perhaps a denial that falls far short of revealing the sincerity of a plant collector but may impress the critical outsider is the fact that plant collections habitually are made in multiplicate sets bearing identical serial numbers for purposes of sale or exchange amongst the numerous botanical institutions of the world. It would be difficult indeed for even an unusually perverse individual to pursue his passion under such adverse circumstances. The chief danger in plant collecting actually is that of choosing too many "normal" specimens. The statistical errors from such likelihood, however, should be ineffective.

"Mass collections," which I prefer to call "local population samples," have been advocated recently by Anderson (1941) and others as an aid to the solution of certain systematic and cytogenetic problems. This method of sampling local variation surely is a very useful one, and a tool which I have used in part in my own work. Certain attendant disadvantages should be discussed, however.

It is known, for example, that the phenotypic responses to the fluctuations of climate may vary from year to year in a given place, as Lewis (1947) recently has shown with respect to *Delphinium*. Population statistics obtained from a given locality for a given year may not be compared safely with samples from other localities at another time, perhaps even during the same year. Employing only local population samples, the task of effectively covering the entire range of a single widespread species, in the case of *Asclepias tuberosa* about 1,500,000 square miles, assumes fantastic proportions.

The most reliable statistics concerning plant populations over a wide area must be made not during a single season but over a span of years, and the samples must be randomly selected and as widely distributed as only generations of differently tempered naturalists can accumulate them. It is possible to meet these requirements only by the use of herbarium collections. It is not a new convenience: plant taxonomists have been enjoying it since long before the birth of Linnaeus.

The advocate of "mass collections" may retort that even though herbarium samples may cover distribution in time and space more effectively, the samples are smaller at best than those specially made by his methods. The statistical fallacy of this argument is obvious. The reader should not infer that I am condemning the use of local population samples. I am merely attempting to point out what I consider to be their limitations and to defend my use of herbarium specimens. I have obtained quite interesting results through using both methods coordinately.

Perhaps this will be an appropriate place to caution firmly against the inconsiderate use of herbarium material for statistical work. Being an herbarium custodian myself I can anticipate the angry protests which will arise from my colleagues at the prospect of their precious charges being plucked, petal by petal, or for that matter, leaf by leaf, by increasing numbers of "biosystematists." We may not treat herbarium specimens as we would living plants having the power of regeneration of lost parts. Type or other authentic specimens must remain sacrosanct for the use of posterity. Only abundant parts of herbarium specimens should be sampled in studies such as these, and then only by an experienced student upon express permission of the proper authority.

Being an herbarium man, my first impulse in beginning my study of leaf variation in *Asclepias tuberosa* was to turn to the herbarium of the Missouri Botanical Garden where I am employed. There I found several hundred sheets of specimens representative of the entire range of the species. Nearly all the sheets I found to bear at least one entire stem of the plant. The leaves of each, habitually numerous, I found to be well preserved, being somewhat leathery in texture. Since they were so abundant, I discovered that at least some had escaped being glued to the paper and could be removed without appreciably damaging the specimen.

After experiment I adopted the procedure of selecting a "random" leaf from about the middle of a single flowering stem of each specimen, if it included more than one stem, and recording the locality (state and county for reasons which will develop) from whence it came. I soon found also that it is desirable to keep a record of the various collectors' numbers in order to avoid statistical bias from measurement of duplicated specimens so prevalent in large herbaria. This entails no unusual inconvenience, being a common monographic practice. The leaves were boiled in water, separately, until completely exhausted of air. Their outlines were then traced upon paper with a sharp 2-H lead drawing pencil, using an illuminated tracing table.

For tracing, I have found best adapted to my needs the large sheets of millimeter grid paper printed by Keuffel & Esser of New York. The 5- and 10-millimeter lines are specially accentuated on this paper, which facilitates both orientation of the tracings and subsequent measurement. The grid paper may be protected from the moistened leaf by placing between them a small piece of wax paper.

To some, I might appear to have been more scientific had I used some photographic means of transferring the leaf outlines. There are several advantages of the tracings, the first of which is the millimeter grid itself, special advantages of which will be indicated. A second advantage is that the tracings can be added to the large grid sheets consecutively as they accumulate, assigning a special sheet to each local population sample, or particular geographic division. In short, the tracings appeared to be more convenient and photographs or blueprints unnecessarily complicated and time-consuming. In measuring smaller objects, greater accuracy doubtless would be obtained by the latter methods. The degree of accuracy obtained through tracing will be discussed presently; I believe that it will be found sufficient for my needs.

QUANTITATIVE MEASURES

It has been explained in previous paragraphs that the chief, if not the only, criteria distinguishing the three subspecies of *A. tuberosa* are found in differences of leaf shape. Size, as measured by median length and width, is of minor taxonomic importance except perhaps in providing abstract universe values. This is usually true because size, although it has a genetic basis, is more directly influenced by environment and age of organism than is shape.

It is easily seen in fig. 2, which consists of very small random samples of leaves, that leaves of ssp. *tuberosa* may be said to be of greatest average width and those of ssp. *interior* of greatest average length, while those of ssp. *Rolfsii* average least in both regards. But an experienced plant systematist probably would prefer to point out that the leaves of *tuberosa* tend to be broadest above the middle (obovate to oblanceolate) with rounded or tapered base, those of *interior* broadest below the middle (lanceolate to ovate-lanceolate), usually with 2-lobed (cordate) base, and those of *Rolfsii* more or less fiddle-shaped (pandurate) and with crisped margins.

Determined to find a suitable continuous scale with which to measure leaf shape in *Asclepias tuberosa,* I finally recognized that the differences in shape, at least those distinguishing ssp. *tuberosa* and ssp. *interior,* resolve themselves into relative differences in width at two points, at approximately one-quarter the median length from the apex and the same distance from the base, respectively. It was obvious that in *tuberosa* the greater width typically is at the upper quarter and in *interior* at the lower quarter. The intergrades usually are found to bear essentially oblong or elliptic leaves, their widths at the upper and lower quarters being approximately equal.

For some time thereafter I measured leaf widths at exactly the upper and the lower quarters of median length, hoping that by the ratios I might be able to distinguish quantitatively the leaves of the two subspecies with respect to unity as represented by the oblong or elliptic leaves of intergrades. This activity ceased when I realized that ratios such as those I was employing are functions of length. Another disillusioning discovery was that both ratios and their reciprocals afford warped scales, and furthermore the warping of the two scales is unequal. I mention these points for the consideration of any who may contemplate using similar ratios in biometric studies.

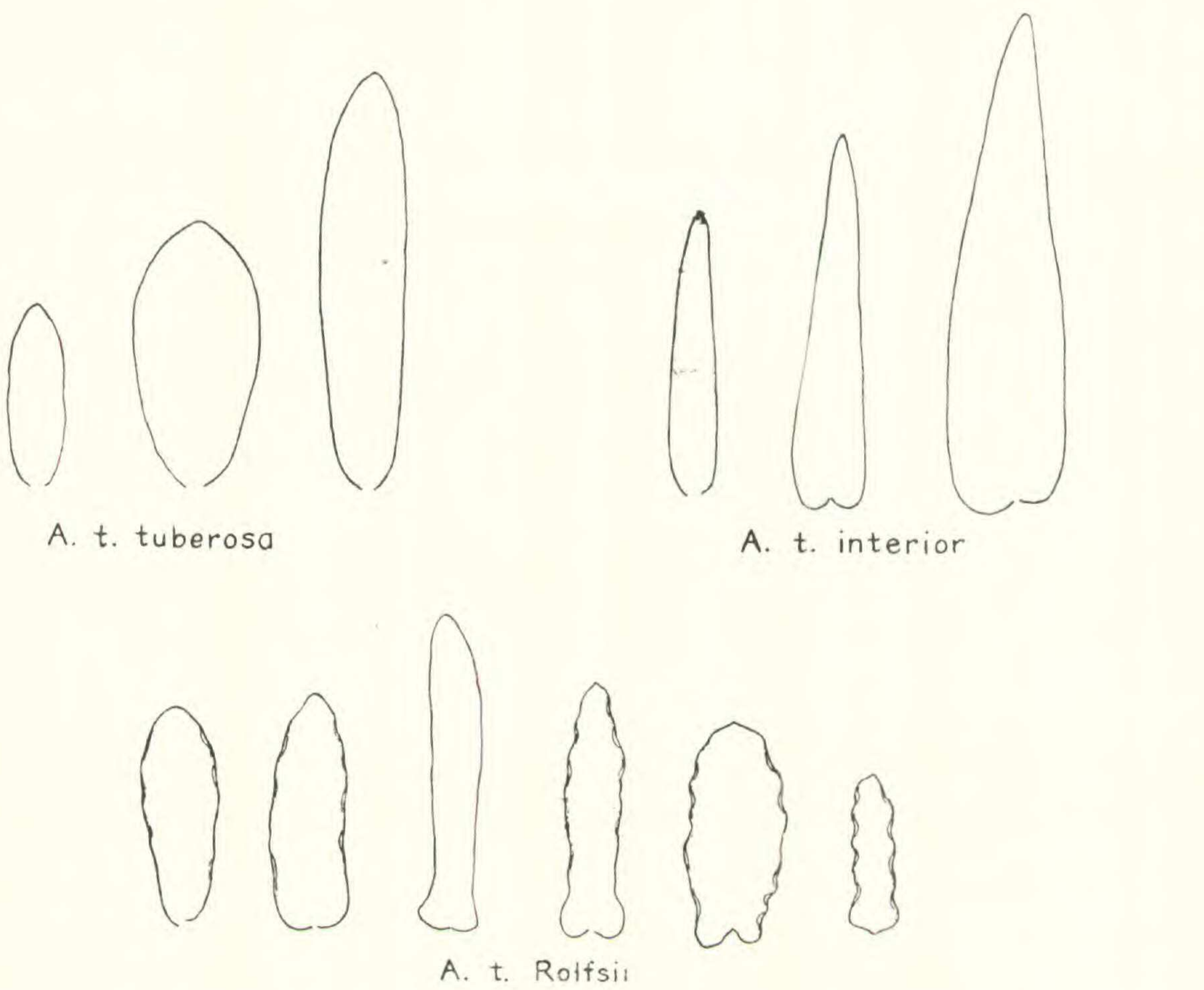


Fig. 2. Representative leaf types of three subspecies of *Asclepias tuberosa*.

The methods which I finally adopted for measuring shape are illustrated in fig. 3. In the diagram to the left of the figure, *AOB* represents the frame by which leaf outlines are oriented at equal distances upon my large grid sheets. The base of the leaf blade, where it joins the petiole, is placed at *O* and the tip vertically above in the position designated as *B*. After tracing the outline about the frame *AOB*, it is a very easy matter, since 1-, 5-, and 10-mm. distances are indicated on the grid itself, to measure median length to the nearest millimeter as the distance *OB*, rounding to the nearest even figure. Median width, *MM'*, is measured also to the nearest millimeter, at the point midway between *O* and *B*, rounding as

before. It appears unnecessary to read these distances to fractions of a millimeter in the light of what we shall learn concerning the experimental error involved.

It will be recalled that leaf shape differences of the two subspecies are found not only in the relative width of the blade at the upper and lower quarter lengths but also in the fact that the blade predominantly is cuneate in *A. t. tuberosa* (fig. 3, center figure) and cordate in *A. t. interior* (fig. 3, right figure). To measure either character it is found desirable to draw a horizontal line at right angles to the median line *OB* at one quarter the distance of its length from the apex *(XX')* and base *(YY')*, respectively.

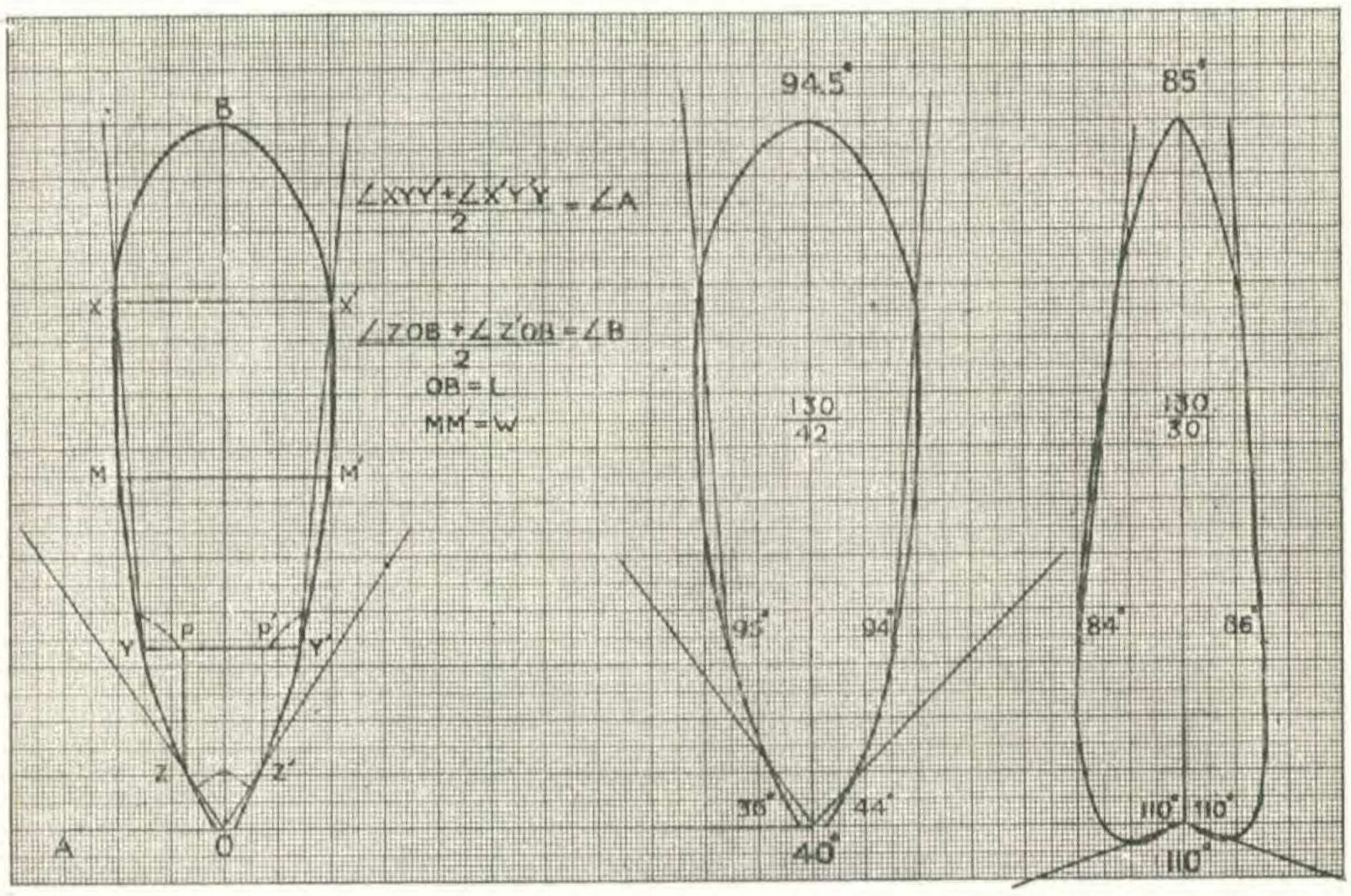


Fig. 3. Methods for measuring leaf shape in butterflyweeds.—Explanation in the text.

In order to measure the direction and extent of apical taper of the leaves two chords now are drawn, XY and $X'Y'$. Using a standard protractor the two angles XYY' and$X'Y'Y$ are measured to the nearest degree, rounding to the nearest even figure, and their mean is entered as the statistic hereafter to be known as $\angle$A.

In fig. 3 it will be seen that measurements of $\angle$A are 94.5° and 85° (treated as 85.0° in computations) for *A. t. tuberosa* and *A. t. interior* respectively. By use of this type of measure, a plant taxonomist will recognize that a leaf of ovate type will always have an angular reading of less than 90°, a leaf of obovate type one of more than 90°, and a leaf exactly of oblong type a reading of exactly 90°.

An angular measure to distinguish different types of leaf base in butterflyweed was obtained after it was recognized that in cordate leaves the tip of the basal lobe usually occurs at a point about midway between *O* and *Y* on the one side, and between *O* and *Y'* on the other. Consequently, I now drop two perpendiculars *PZ* and *P'Z'* at points on *YY'* midway between *OB* and the margin of the leaf as indicated in the diagrams to the left of fig. 3. The angles *ZOB* and *Z'OB* are now

read by protractor as before, and the mean rendered as ∠B, the measure of the leaf base. In the diagrams to the center and right of fig. 3 it is seen that the example for the cuneate base of ssp. *tuberosa* has an ∠B value of 40° while the equivalent value for the cordate base of ssp. *interior* is 110°. A truncate base would have an ∠B of 90°. In computations these figures are recorded as though significant to one decimal.

It will occur to the reader that the values ∠A and ∠B actually refer to hypothetical leaf halves and thus are not real variables. Such is doubtless the case, but their other virtues will probably save them from being condemned by the practical statistician. In addition, my recording of the mean angles to one decimal in excess of significant digits is open to criticism although I believe it will be allowed since subsequent computations are limited to one decimal. In practice the process of averaging, besides halving the scale intervals, has the effect of halving the experimental error.

Although ∠A and ∠B have been very satisfactory as measures for shape in *A. t. tuberosa* and *A. t. interior*, I must confess that they are wholly inoperative with respect to *A. t. Rolfsii*. This has been a great disappointment, although to be anticipated since one could scarcely expect to differentiate three value ranges and all their intermediates upon a linear scale. This is an unfortunate consequence of the biological reality of *Rolfsii*. It might be possible to exclude *Rolfsii* from the absolute comparison of *tuberosa* and *interior* and yet to contrast it with both by means of an additional system of arbitrary scores, say for the crisped margin of the leaf. This would mix a discrete with four continuous scales, however, and the result probably would not be very helpful.

There can be little doubt that *Rolfsii* interbreeds with both *tuberosa* and *interior* upon the southeastern coastal plain, and it would be interesting to be able to measure the phenomenon accurately. It is possible to do so only indirectly according to my methods. In further studies we shall not forget the role that *Rolfsii* undoubtedly plays, particularly with regard to introgression with the other two subspecies, but we will be able to deal with it only through inference.

ESTIMATES OF EXPERIMENTAL ERROR

The methods just described at one time appeared so crude to me, compared to the technical refinements of others, that I spent some effort in obtaining estimates of the experimental error involved. Despite the risk of being tedious, I am reporting the results in some detail because I believe that exercises of this sort should be published more frequently. As a matter of fact, I know of only one other published estimate of experimental error of measurements used in population studies, that of Sumner (1927), in which the author was chiefly interested in variation of measurement amongst different observers.

In the summer of 1945 ten leaves of *Asclepias tuberosa interior* were collected along a roadside near Valley Park, St. Louis County, Missouri. They were placed in numbered envelopes and subsequently measured with respect to length, width,

∠A and ∠B, while in the fresh condition. After measurement, each leaf was returned to its proper envelope and dried under pressure for a week. For ten consecutive days thereafter the leaves were drawn and measured, being returned to their proper envelopes each time, but the order of the envelopes changed by shuffling. After the tenth dry measurement the leaves were boiled separately and measured a last time. In this experiment extra precaution was taken against unconscious bias in that I personally traced the outlines on each occasion, while my friend Richard W. Holm performed the actual measurements independently.

Table I contrasts the measurements of the ten leaves in the fresh condition and after having been boiled after drying. Table II presents the results of measuring the ten leaves upon ten different occasions. The first is designed to show, as far as this case is concerned, how comparable statistics obtained from fresh leaves and those from soaked herbarium specimens may be. The second is a gage of accuracy in the tracing and measuring process itself, and also provides something of a guide to the statistics of Table I.

TABLE I

MEASUREMENTS OF *ASCLEPIAS TUBEROSA INTERIOR* LEAVES WHEN FRESH AND AFTER SOAKING IN BOILING WATER

(Means, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

		∠A			∠B			Length			Width		
	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
Fresh	10	85.0	0.5	0.6	120.0	1.6	1.3	77.3	1.4	1.8	19.7	0.5	2.5
Soaked	10	85.2	0.4	0.5	120.6	2.1	1.7	76.1	1.3	1.7	19.3	0.5	2.6

Since I have no similar exercises with which to compare, it is hard to evaluate the results recorded in Table II. I was surprised indeed, however, when the error appeared to be so small, in view of my rather crude instruments, ranging from 0.4° or 0.4 per cent for ∠A to only 1.5° or 1.3 per cent for ∠B. The metric error likewise appears to be small. In comparing Table I with the discussion of Table II it is seen to be immaterial, as far as the two angles are concerned, whether the leaves are measured fresh, dry, or soaked, since all three means for both lie within the experimental error estimated in Table II. In length and width, on the other hand, the three means lie at distances greater than that provided for by the estimate of error, particularly in width. This is disquieting, but there is no recourse since it would be impossible to measure all leaves while fresh. Statistics of length and width, however, will play a role subordinate to those for the two angles in the studies which follow, since they are not important systematically.

TABLE II

MEASUREMENTS OF TEN DRIED LEAVES OF *ASCLEPIAS TUBEROSA INTERIOR* MEASURED ON TEN CONSECUTIVE DAYS

(Means, standard deviations, coefficients of variation, means of means, means of standard deviations, and means of coefficients of variation; angles in degrees, length and width in millimeters)

Leaf No.	∠A			∠B			Length			Width		
	$\overline{X}$	s	V	$\overline{X}$	s	V	$\overline{X}$	s	V	$\overline{X}$	s	V
1	85.2	0.2	0.2	118.9	1.2	1.0	76.0	0.0	0.0	20.0	0.0	0.0
2	85.2	0.4	0.5	117.2	2.0	1.7	75.2	0.4	0.5	18.0	0.0	0.0
3	85.1	0.3	0.4	119.1	1.9	1.6	75.9	0.4	0.5	18.6	0.5	2.7
4	85.3	0.3	0.4	121.5	1.4	1.2	75.4	0.5	0.7	19.0	0.0	0.0
5	85.4	0.4	0.5	119.6	2.7	2.2	75.6	0.5	0.7	18.7	0.5	2.7
6	85.2	0.6	0.7	114.0	1.2	1.0	73.2	0.4	0.5	19.0	0.0	0.0
7	85.3	0.4	0.5	117.2	1.1	0.9	74.0	0.0	0.0	18.1	0.3	1.7
8	85.1	0.2	0.2	120.6	1.3	1.1	77.1	0.3	0.4	19.1	0.3	1.6
9	85.1	0.5	0.6	113.9	1.6	1.4	75.3	0.5	0.7	18.1	0.3	1.7
10	85.1	0.3	0.4	121.8	1.0	0.8	72.6	0.8	1.1	18.0	0.0	0.0
$\overline{X}$	*85.2*	*0.4*	*0.4*	*118.4*	*1.5*	*1.3*	*75.0*	*0.4*	*0.5*	*18.7*	*0.2*	*1.0*

IV. The Phenocontours

Technique of mapping

Phenocontour mapping is such a recent biological technique that it may be worth while to combine the account of my own practice with some general comments. The subject may be divided into several considerations which impinge upon one another so closely that they form a sort of continuum. In beginning an investigation of this kind, the first thing to be done is to become familiar with the systematic morphology of the organism chosen for study. Without a clear understanding of the critical characters of the species, for example, much time may be spent measuring size which might be spent more profitably measuring shape. In plant subjects, recourse should be had to a large, well-ordered, general herbarium where the problem in all likelihood can be viewed in perspective and plans made for the most promising direction of attack.

Having selected a problem and noting the most advantageous direction of attack, suitable biometric measures must be devised as the *sine qua non* of all that is to follow. A measure must be found which expresses numerically the phenomena judged as biologically most significant. Any given measure will only infrequently be found effective for more than the organism for which it was invented. My method of measuring leaf base in *Asclepias tuberosa*, for example, may be quite useless in measuring that of another species.

A good measure should be duplicable, sensitive to organic variation, and should provide an unwarped scale. These are rather complex attributes to discuss briefly.

They discriminate, in my opinion, against various types of discontinuous scales encountered in arbitrary scoring. In some cases, as in presence-or-absence criteria, scoring is the only sensible procedure. In others, the varying characters may be so complex that scores at first would appear as the only recourse. But scores almost inevitably are the product of the personal equation and should be used only when standard scales, such as the linear and the angular, are unavailing. The statistical advantages of fixed continuous scales are expressed most succinctly by Miss Walker (1943): "In order to know how much of a trait an individual has or to say that one thing is twice another, it is necessary not only to have equality of units but also to establish a zero point. Only when these two conditions are met can scores properly be spoken of as measures."

The area chosen for mapping preferably should include the entire range of the species or other taxonomic unit under investigation. This sometimes will be very large and impose considerable handicap in the gathering of data. But as a general rule the biological interest will be proportional to the area because of the relative number of factors allowed to operate. When I commenced this study of butterflyweed several years ago, I seriously considered following a suggestion of Huxley and confining my efforts to a single profile across the distribution of the species. Luckily my taxonomic training insisted that the distribution be treated as a whole; several unsuspected topics of interest emerged as a result.

Equal to the importance of adequate measures is that of adequate sampling. The prime requisite of sampling is that it be random. In biometric work of this kind, one cannot use the word "random" in quite the same sense in which it is employed in ordinary statistics; one cannot make use, for example, of the published lists of random numbers commonly employed in sampling. It is necessary to avoid the selection of cases which exhibit injury or manifest growth abnormality. It is necessary also to select cases at equivalent stages of development; therefore I have selected leaves from about the middle of a flowering stem rather than leaves at a given node from the top or bottom of the stem, for some stems produce a larger number of nodes during the course of their development than do others. Above all, one must not allow himself to select what he chooses to call "typical" cases in the hope of deriving therefrom the benefits of random sampling.

It does not seem quite possible to deal with questions of bias here in the ordinary way. In my own studies I think of bias as being intellectual, accidental, or biological. The intellectual bias is understood easily as the more or less subconscious desire to vindicate a predisposition. Perhaps its best antidote is to remember that truth may be stranger than fiction. Accidental bias may be occasioned by the paucity of specimens available for study in a given population. If herbarium specimens are in use it may be occasioned by duplicated specimens frequently encountered. Protection is taken against this by keeping a list of collectors' numbers as in ordinary monographic work. A variety of other sources of accidental bias come to mind.

Biological bias is a phenomenon which is less easy for a mathematical statistician to anticipate. In plants, if a species forms true clons it may be difficult if not impossible to tell whether one actually is sampling a number of genetic individuals or offshoots from a single plant. Fluctuations of climate are known to have a pronounced effect upon phenotypic expression (Lewis, 1947), and a sampling made during any given season or year may be biased as a result. Sampling made for convenience along roadsides or in occupied areas may present a very special bias (Wiegand, 1935). On first consideration it might be thought possible to escape physiological bias if sampling of an organism were made at random stages of its seasonal growth. But if any sample is allowed to consist chiefly of cases collected during a given stage of development, it may be biased with respect to others made during another stage. I have limited my sampling of butterflyweed to plants in full anthesis.

The number of samples and number of cases included is secondary in importance to the degree of randomness obtained. However, it may be worth while to emphasize that an adequate sampling is dependent more upon the number and randomness of samples than upon the number of included cases. Of course I do not overlook the fact that reliability of means and their derived statistical measures of variability increases as a rule with sample size; but size alone is not an indication of randomness and hence of reliability. Adequacy of sample size is determined by the unique degree of variability of each organism and can be determined in each case only after special observation.

Adequate sampling of the vast distribution of such a species as *Asclepias tuberosa*, an area of approximately 1,500,000 square miles, is clearly beyond the power of a single individual since we require randomness of climate, time, and environment. In an earlier section of this paper I have explained how herbarium collections would appear to satisfy these conditions. The argument may be advanced, however, that the relatively small numbers of specimens available in herbaria is insufficient for an adequate sampling distribution. Superficially it appears small indeed. Its adequacy with regard to butterflyweed may be judged by fig. 7 of this paper, in which statistics of two sets of samples are compared: one from the herbarium, consisting of 117 cases distributed along an approximately 1200-mile profile from Topeka, Kansas, to Norfolk, Virginia, and the other of 994 cases collected personally by myself and two friends in June, 1946, along roadsides between those two cities. The close correspondence and consistency of the two samplings are striking.

If I may extend my comments on sampling a bit further, I should like to call attention again to the area inhabited by *A. tuberosa*: approximately 1,500,000 square miles. First impulse might be to obtain statistics from whatever source and to combine them for the supposed benefits of larger samples. I am obliged to confess that for this vast area I have been able to collect and measure only approximately 12,000 cases in the time at my disposal, or about 1 per 115 square

miles. At first glance this appears inadequate indeed, and it minimizes the true situation since the cases could not, for practical reasons, be distributed uniformly. Actually my samples fall into three rough categories: cases obtained from herbarium specimens, those collected along roadsides, and those obtained in hit-or-miss fashion throughout the whole species distribution, largely through the kindness of interested friends.

Cases obtained from these three sources surely cannot be combined, since they have been accumulated under different conditions, and their discrepant numbers would constitute a serious bias. Consequently I have kept them separate although using all for comparison according to the special values accrued from each. At the risk of over-emphasis, I should like to repeat that of these three categories of samples, I consider that obtained from herbarium material by far the most representative biologically although they are also the smallest numerically, numbering only about 3,000 cases, or somewhat less than 1 per 470 square miles of the specific distribution. As shocking as this ratio will appear, I believe the derived statistics, on the whole, to be biologically reliable, and I have used them in constructing my phenocontour maps to the exclusion of other data.

The projection of data upon a phenocontour map is a rather complex matter which depends upon such factors as amount of available statistics, size and character of the area involved, and nature of the information which it is desired to convey. In his study of pelage melanism in the Tasmanian bush opposum, *Trichosurus vulpecula fuliginosus*, Pearson (1938) employed relative percentages of two class scores, black and gray, although he mentions unmeasured variation in both. By using commercial pelt records of approximately 105,000 cases distributed amongst 48 more or less equally spaced stations, a ratio of about 5 cases per square mile, he was able to plot a series of four contours ("isophenes" of Huxley) approximately separating areas including 0–25 per cent, 25–50 per cent, 50–75 per cent, and 75–100 per cent of gray pelts. His conclusions are chiefly historical.

Few biologists will be able to equal the volume of Pearson's data. To be as representative of distribution for *Asclepias tuberosa*, my records would have to embrace over 7,000,000 cases, instead of the approximately 3,000 which I have! Another advantage of Pearson's data is the distribution of cases amongst 48 rather equally spaced stations.

Readers familiar with the composition of a general herbarium already are aware that the geographical distribution of exsiccatae, even in the United States, is far from uniform. Greatest concentrations of specimens occur as a rule about well-established cities where botanists long since have resided. Next come states which have undergone systematic botanical surveys, and there is a gratifying number of these. Thirdly, there are regions of peculiar scenic or biological interests, such as our national parks, which attract appreciable numbers of plant collectors. But we cannot disregard areas, sometimes of considerable extent, where a lamentable hiatus

of herbarium records is encountered. There is no fixed pattern to this mosaic, and it presents the major obstacle in phenocontour mapping from herbarium collections.

The projection of data upon a phenocontour map presumably should require the imposition of equidistant statistics from equal areas. I have accomplished this by dividing the species distribution into quadrats of equal areas for which I have combined the data secured from the various localities included within each. This, of course, creates a system of artificial (in contrast to natural) populations from which the desired statistics are computed.

The quadrat area chosen clearly depends upon the geographic plasticity of the species and the nature of the information desired. If the species is very responsive to altitude or ecology, the size of the quadrat will need to be much smaller than if the organism is not so sensitive. This may be a very serious obstacle in mapping a large area. Fortunately, *Asclepias tuberosa* appears to be rather indifferent in these respects, and the size of the quadrat depends chiefly upon the necessity of obtaining artificial populations equally distributed and yet of sufficient numbers for statistical analysis. This amounts to a certain guise of "gerrymandering," but is legitimate since the same quadrat area is employed throughout.

In this study of butterflyweed I have manipulated quadrat area to the end of obtaining populations of at least five cases in critical but poorly collected regions. The quadrats in this instance are approximately 120 miles square, and there are 136 within the range of *A. t. tuberosa* and *A. t. interior*—many fewer than I would wish. Even with these large areas, it will be seen that certain of them have failed to yield as many as five cases. After recording the quadrat data, isophenes may be drawn, if desired or possible, either connecting equal statistics or according to arbitrary ranges, as practiced by Pearson.

The nature of statistics projected upon the map will vary with individual problems and with the inclination of investigators. If scores are used, Pearson's system, already explained, would appear admirable. If a continuous scale has been employed in measurement, it will be natural to compute the mean; and from it may be derived any of the familiar measures of dispersion such as the standard deviation and the coefficient of variation. These may be entered on the map together with the mean. A measure of variability frequently will be necessary in order to interpret the geographical distribution of means.

Of course there is a vast number of statistical formulae which may be used for the analysis of biological measurement, and if one has a taste for mathematics the possibilities are endless. In my own study, after some dalliance, I have limited myself, as a rule, to the simple calculation of means, standard errors, standard deviations, and coefficients of variation, the second and fourth largely for the sake of convention. An outstanding example of another point of view is afforded by

Czeczottowa's (1933) remarkably painstaking study of variation in beech leaves, to which Dr. M. K. Elias kindly has called my attention.

In the phenocontour maps which follow, quadrats containing five or more cases are indicated with the mean in large bold face type and the associated standard deviation in large italics. Means of quadrats containing less than five cases are printed in small Roman type. The standard deviation is used instead of the coefficient of variation because there appears to be no need for percentage comparison; also the former adapts itself more readily to my procedure, and the latter appears too sensitive to the relative magnitudes of the means, in addition to other disadvantages (cf. Kesteven, 1946).

INTERPRETATION OF THE MAPS

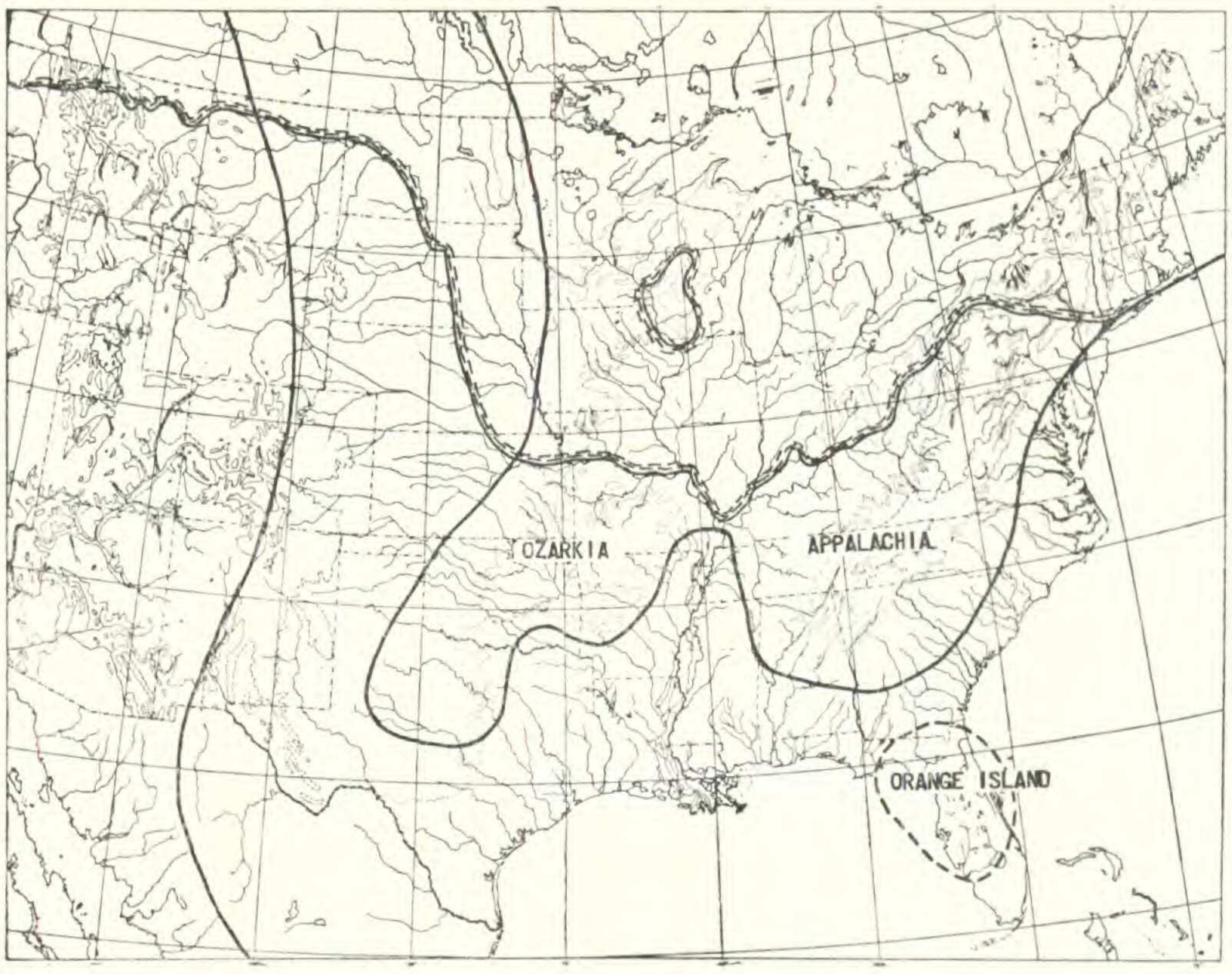
INTRODUCTION

Before turning to the phenocontour maps, it may be well to consider very hastily certain details of the paleogeography of eastern North America which will have a bearing on our interpretations of the population dynamics of *Asclepias tuberosa*. The discussion is illustrated by Map II.

It is generally recognized that many of the principal families of Flowering Plants were established by the close of the Mesozoic era, possibly before the Lower Cretaceous. Although I know of no indubitable fossil remains of *Asclepias*, numerous records of Late Cretaceous and Mesozoic imprints, such as the form genus *Apocynophyllum*, are known which may well represent, at least in part, ancestors of our modern milkweeds, if not records of extant species. At any rate, present distributions of many species of *Asclepias* correspond so closely to what is known of Cretaceous geography that I feel we may hypothesize rather safely much the same speciation in those times as that with which we are familiar at present (cf. Woodson, 1947).

The Cretaceous has been called "the age of greatest submergence of the continents and the most extensive epeiric seas the Earth has known (Schuchert & Dunbar, 1933)." The complex submergences and resulting isolation of floras probably were of the utmost importance to the meteoric evolutionary diversification of Angiosperms during this time, and are reflected in present speciation.

Late Cretaceous saw the climax of the dissection of North America with the submergence of the Rocky Mountain trough from the Caribbean to the Arctic. This was accompanied by submergence of the southeastern coastal plain, particularly north of the Gulf of Mexico, a deep embayment extending up the present Mississippi valley as far as southern Illinois. This embayment separated the ancient Appalachian and Ozark plateaus, including the extension of the latter to the Llano uplift in central Texas, and is recalled in our present vegetation by numerous vicarious species and subspecies. Amongst these may be mentioned *Asclepias t. tuberosa* and *A. t. interior*, respectively.

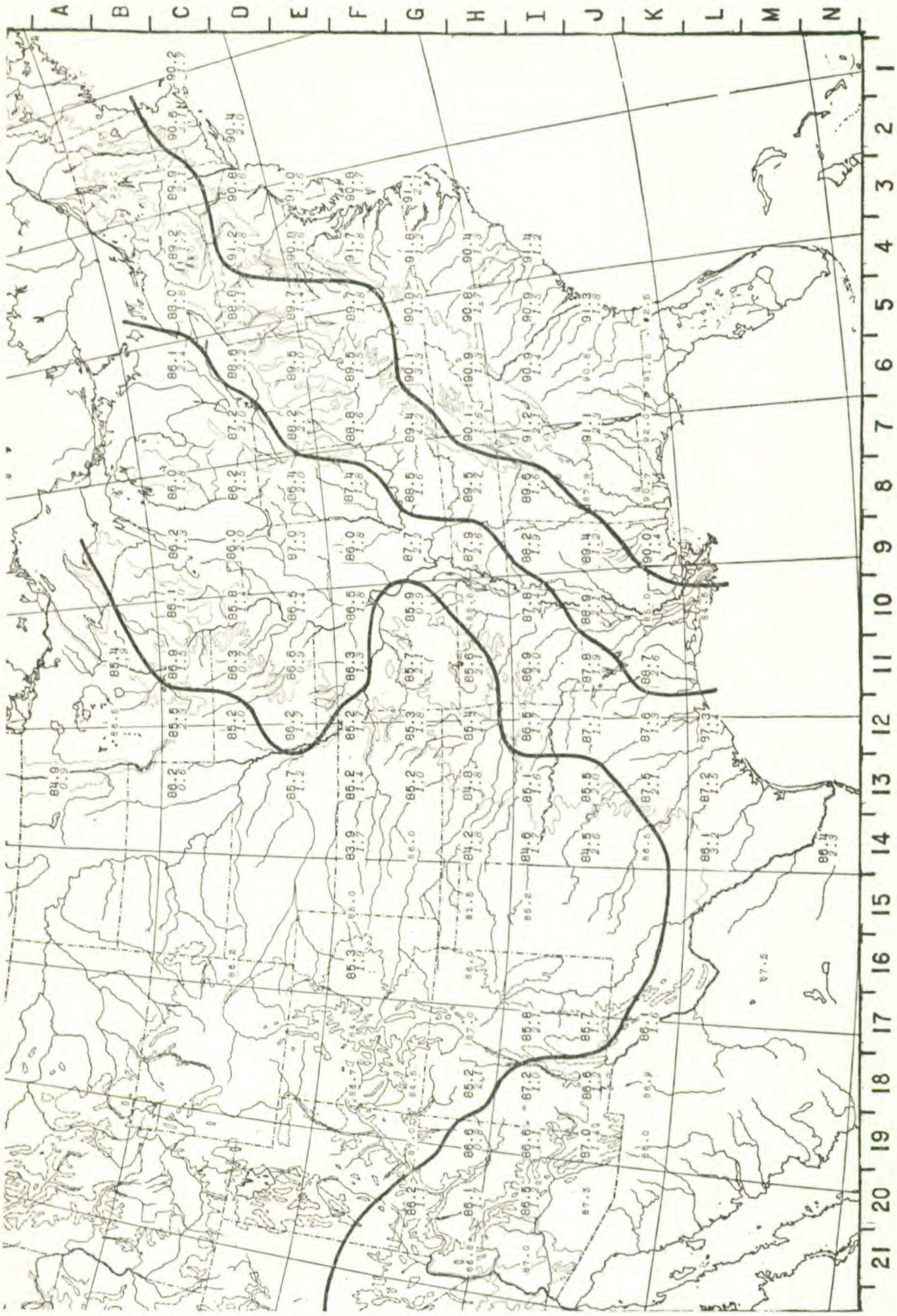


Map II. Ozarkia, Appalachia, and Orange Island, with reference to the Cretaceous and early Mesozoic seas, and Pleistocene glaciation. Explanation in the text.

Of equal interest in this connection is the probably fluctuating emergence of low islands in what is now northern Florida, culminating in the early Cenozoic in the appearance of the more sizable "Orange Island," separated from the Georgian coast by the Suwanee strait (Schuchert, 1935). On these islands possibly developed many or most of the Floridian endemics of Appalachian affinity, including *A. t. Rolfsii* and numerous other milkweeds.

Withdrawal of the Cretaceous seas during the early Cenozoic effected the reunion of the Appalachian and Ozarkian lands in Oligocene, and of emergent Orange Island to the continent in Pliocene. By Pliocene, therefore, there apparently were no geographic barriers to reunion of the disjunct distributions of the three subspecies of *Asclepias tuberosa,* if indeed they existed at that time.

Pleistocene brought the continental ice sheets approximately to the present valleys of the Missouri and Ohio rivers, virtually to the head of the old Mississippi embayment of Cretaceous and early Cenozoic times. This undoubtedly provided a partial secondary separation of the putative ranges of *A. t. tuberosa* and *A. t. interior*. It is well known that four glacial periods occurred during Pleistocene, interspersed by warm interglacials longer, indeed, than the present day is removed from the last withdrawal of the ice. The time since the retreat of the Wisconsin ice sheet usually is reckoned at about 25,000 years.



Map III. *Asclepias tuberosa*: phenocontour system of ∠A (apical taper of leaves). Explanation in the text.

These well-known facts are outlined to give perspective for what we are to find in the population dynamics of *Asclepias tuberosa* in recent times. They underline the possibility that the phenomena which we will discuss are not unique to the present, but perhaps the repetition of past and similar phenomena. It is difficult indeed to estimate the effect of such repetitions upon population genetics, but at least they should not be disregarded.

∠A

The phenocontours for ∠A which are reproduced in Map III are projected according to quadrats 120 miles square, as has been explained previously, with the means of quadrat populations including five or more cases printed in large bold-face numerals and the associated standard deviations immediately below in large italics. Means of quadrat populations including less than five cases appear in small Roman-type numerals. Three isophenes have been drawn approximately separating bold-face means included within intervals of 2° from the Atlantic coast. Statistical sources for the data used in compiling this map, as well as for the three which follow, are presented in Table III.

It may be considered that the 90°–91° contour represents the range of "true" *A. t. tuberosa,* while that of "true" *A. t. interior* is indicated by the 84°–85° contour. The 88°–89° and the 86°–87° contours represent subspecific intermediates except the populations in the far southwest and for the most part in the northern Mississippi valley which, for reasons to be developed later, are regarded as affected by intra-subspecific differentiation. Data for *A. t. Rolfsii* regrettably are absent for reasons already explained.

After the preceding discussion of paleogeography, it is easy to identify the central portions of the "true" subspecies distributions as centering in general on the Appalachian and Ozarkian-Llanoan headlands of Late Cretaceous time. Between these centers a broad cline stretches from the Great Lakes to the Gulf of Mexico, broader in the northern and abruptly constricted in the southern halves.

The most obvious explanation of this cline is the hybridization of individuals of either subspecies at the commissure of their distributions with continuous backcrossing to obtain the remarkably broad phenotypic gradient presented by the map. This process has been termed "introgressive hybridization" by Anderson and Hubricht (1938), shortened to "introgression" by some recent writers, and the result is a genocline (Huxley, 1942).

The middle isophene apparently represents the mid-current of gene flow between the two subspecies. Its virtually straight course is striking, and possibly would suggest nearly equal introgressive pressure from east and west. The nearly rectilinear nature of this isophene is the only evidence that will be presented at this time to support my assertion that the peculiar course of the western isophene is due to intra-subspecific forces operating within *A. t. interior*, and not to intro-

TABLE III

LEAVES OF *ASCLEPIAS TUBEROSA* (SENSU LAT.) FROM HERBARIUM MATERIAL ASSEMBLED INTO EQUAL-AREA QUADRATS ACCORDING TO GEOGRAPHIC PROVENIENCE

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
A-13	5	84.9 ± 0.4	0.9	1.1	95.2 ± 7.3	14.7	15.4	79.8 ± 3.6	7.3	9.1	13.0 ± 1.8	3.7	28.5
B-3	4	90.0			40.9			83.5			12.8		
B-11	9	85.4 ± 0.7	1.9	2.2	84.7 ± 4.8	13.4	15.8	79.4 ± 2.4	6.9	8.7	13.0 ± 1.4	3.9	30.0
B-12	3	86.5			100.0			78.0			8.7		
C-1	21	90.2 ± 0.4	1.7	1.9	48.4 ± 3.0	13.2	27.3	68.8 ± 2.9	12.9	18.8	14.6 ± 1.1	5.0	34.2
C-2	60	90.6 ± 0.3	2.1	2.3	48.1 ± 2.0	15.0	31.2	79.3 ± 2.1	16.4	20.7	17.8 ± 0.8	5.8	32.6
C-3	23	89.9 ± 0.4	2.1	2.3	63.3 ± 4.0	18.6	29.4	89.2 ± 3.7	17.4	19.5	17.8 ± 0.9	4.3	24.2
C-4	26	89.2 ± 0.3	1.7	1.9	64.0 ± 4.5	22.6	35.3	82.2 ± 2.7	13.6	16.5	12.9 ± 0.8	3.8	29.4
C-5	14	88.0 ± 0.5	1.8	2.0	74.7 ± 5.4	19.4	26.0	85.4 ± 4.8	17.1	20.0	15.4 ± 1.3	4.8	31.2
C-6	9	86.1 ± 0.8	2.4	2.8	83.6 ± 4.7	13.3	15.9	73.7 ± 5.2	14.6	19.8	15.3 ± 1.2	3.4	22.2
C-8	20	86.0 ± 0.4	1.8	2.1	84.4 ± 4.2	18.2	21.6	74.2 ± 1.9	8.4	11.3	12.8 ± 0.8	3.6	28.1
C-9	12	86.2 ± 0.4	1.3	1.5	84.9 ± 6.4	21.3	25.1	78.7 ± 3.5	11.5	14.6	11.8 ± 1.4	4.8	40.7
C-10	16	86.1 ± 0.3	1.0	1.2	91.3 ± 4.3	16.6	18.2	77.8 ± 3.1	12.1	15.6	12.5 ± 1.1	4.1	32.8
C-11	40	86.9 ± 0.2	1.5	1.7	97.3 ± 3.0	18.9	19.4	83.2 ± 2.1	13.1	15.7	11.0 ± 0.5	3.2	18.7
C-12	11	85.5 ± 0.7	2.3	2.7	92.6 ± 4.2	13.4	14.5	81.1 ± 4.6	14.4	17.8	12.0 ± 1.3	4.2	35.0
C-13	5	86.2 ± 0.3	0.6	0.7	95.8 ± 8.1	16.3	17.0	74.8 ± 6.6	13.2	17.6	11.6 ± 0.9	1.8	15.5
D-2	38	90.4 ± 0.3	2.0	2.2	56.9 ± 3.6	21.9	38.5	77.4 ± 1.9	11.4	14.7	17.0 ± 0.8	5.1	30.0
D-3	61	90.8 ± 0.2	1.6	1.8	56.6 ± 2.3	17.6	31.1	73.9 ± 2.1	16.2	21.9	16.9 ± 0.7	5.2	30.8
D-4	30	91.2 ± 0.5	2.8	3.1	58.0 ± 4.8	25.8	44.5	83.4 ± 2.9	15.7	18.8	16.6 ± 1.0	5.2	31.3
D-5	6	88.8 ± 1.4	3.1	3.5	66.0 ± 14.4	32.3	48.9	107.3 ± 11.1	24.8	23.1	19.3 ± 3.2	7.2	37.3
D-6	10	88.6 ± 0.7	2.2	2.5	77.2 ± 8.3	25.0	32.4	86.2 ± 4.7	14.2	16.5	16.1 ± 1.6	4.7	29.2
D-7	39	87.2 ± 0.3	2.0	2.3	82.6 ± 3.4	21.1	25.6	83.6 ± 2.6	16.2	19.4	15.0 ± 0.7	4.6	30.7
D-8	36	86.2 ± 0.2	1.5	1.7	96.4 ± 4.9	29.1	30.2	81.0 ± 2.1	12.4	15.3	15.4 ± 0.7	4.0	26.0
D-9	31	86.0 ± 0.4	2.0	2.3	95.0 ± 2.6	14.2	14.9	80.8 ± 2.1	11.7	14.5	12.2 ± 0.6	3.1	25.4
D-10	19	85.8 ± 0.3	1.4	1.6	93.3 ± 3.4	14.6	15.6	84.7 ± 3.0	12.7	15.0	13.9 ± 0.8	3.5	25.2
D-11	26	86.3 ± 0.2	0.7	0.8	105.5 ± 2.1	10.5	10.0	80.1 ± 3.3	16.6	20.7	11.5 ± 0.7	3.5	30.4

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
D-12	30	85.2 ± 0.2	1.0	1.2	108.5 ± 2.4	12.8	11.8	72.2 ± 1.5	8.1	11.2	11.8 ± 0.6	3.0	25.4
D-16	2	86.2			91.5			77.0			13.0		
E-3	106	91.0 ± 0.2	1.6	1.8	49.0 ± 1.6	16.9	34.5	68.3 ± 1.3	12.9	18.9	15.8 ± 0.4	4.7	29.6
E-4	67	90.8 ± 0.2	1.6	1.8	53.7 ± 2.1	16.8	31.3	73.2 ± 2.0	16.1	22.0	17.3 ± 0.6	5.0	28.9
E-5	76	89.7 ± 0.2	1.4	1.6	57.0 ± 1.9	17.0	29.8	82.3 ± 1.8	15.8	19.2	13.8 ± 0.5	4.7	34.1
E-6	18	89.5 ± 0.5	2.0	2.2	71.5 ± 4.9	20.1	28.1	95.3 ± 3.2	13.4	14.1	18.4 ± 1.2	5.1	27.7
E-7	13	88.2 ± 0.8	2.7	3.1	68.0 ± 4.4	15.1	22.2	83.7 ± 4.4	15.3	18.3	15.9 ± 1.7	5.8	36.5
E-8	48	86.4 ± 0.1	2.0	2.3	96.2 ± 1.1	17.3	18.0	83.5 ± 1.0	15.8	18.9	15.0 ± 0.6	4.2	28.0
E-9	50	87.0 ± 0.2	1.3	1.5	99.0 ± 2.0	14.1	14.1	75.0 ± 1.8	12.8	17.1	12.5 ± 0.5	3.6	28.8
E-10	23	86.5 ± 0.3	1.4	1.6	98.5 ± 3.0	13.9	14.1	85.5 ± 2.7	12.7	14.8	14.6 ± 0.7	3.2	21.9
E-11	11	86.6 ± 0.3	0.9	1.0	103.7 ± 2.9	9.3	8.0	70.5 ± 3.7	11.6	16.4	10.3 ± 1.0	3.3	32.0
E-12	10	86.2 ± 0.2	1.2	1.4	112.2 ± 4.2	12.7	11.3	70.5 ± 3.7	11.0	15.6	9.9 ± 0.8	2.5	25.2
E-13	37	85.7 ± 0.2	1.2	1.4	103.2 ± 1.7	10.0	9.7	74.3 ± 1.8	10.8	14.5	12.8 ± 0.5	3.2	25.0
F-3	8	90.8 ± 0.6	1.7	1.9	55.4 ± 4.0	10.6	19.1	70.2 ± 4.9	13.2	18.5	16.9 ± 1.8	4.7	28.6
F-4	15	91.7 ± 0.5	1.8	2.0	58.7 ± 4.2	15.8	27.9	70.0 ± 2.4	8.8	12.6	17.3 ± 0.9	3.5	20.1
F-5	34	89.7 ± 0.3	1.8	2.0	57.5 ± 3.2	18.0	31.3	78.6 ± 3.1	17.5	23.5	14.6 ± 0.8	4.5	30.8
F-6	32	89.5 ± 0.3	1.5	1.7	61.5 ± 3.1	17.8	20.9	84.7 ± 3.4	18.7	22.1	15.0 ± 0.8	4.2	28.0
F-7	24	88.8 ± 0.3	1.6	1.8	73.0 ± 4.5	21.6	29.6	80.0 ± 2.5	11.9	14.9	15.9 ± 0.8	3.6	22.6
F-8	20	87.4 ± 0.4	1.8	2.1	94.4 ± 4.3	18.7	19.8	90.7 ± 2.8	12.0	13.2	17.8 ± 1.0	4.5	25.2
F-9	26	86.0 ± 0.4	1.8	2.1	98.3 ± 2.9	14.5	14.8	84.4 ± 2.4	11.9	14.1	16.1 ± 1.0	4.8	29.8
F-10	30	86.5 ± 0.3	1.8	2.1	101.8 ± 2.6	13.8	13.6	76.1 ± 2.4	13.0	17.1	16.6 ± 0.9	4.7	28.3
F-11	26	86.3 ± 0.3	1.3	1.5	103.4 ± 1.7	8.3	8.0	79.5 ± 2.0	9.9	12.5	14.6 ± 0.7	3.5	24.0
F-12	29	85.2 ± 0.3	1.7	2.0	109.8 ± 1.8	9.4	8.6	72.9 ± 1.5	8.1	11.1	12.3 ± 0.5	2.7	22.0
F-13	27	85.2 ± 0.3	1.4	1.6	101.2 ± 2.1	10.5	10.4	67.5 ± 2.4	12.1	17.9	12.6 ± 0.7	3.5	27.8
F-14	20	83.9 ± 0.4	1.7	2.0	103.2 ± 1.8	8.2	7.9	58.1 ± 2.2	9.6	16.2	11.4 ± 0.8	3.5	30.7
F-15	1	85.0			96.5			71.0			14.0		
F-16	13	85.3 ± 0.5	1.9	2.2	80.3 ± 6.1	21.0	26.2	71.7 ± 3.9	13.5	18.8	13.0 ± 1.2	4.2	32.3
F-17	1	84.5			93.5			83.0			18.0		
F-18	3	86.7			83.5			76.7			9.0		
G-3	50	91.1 ± 0.3	2.1	2.3	52.8 ± 2.8	19.6	37.1	63.9 ± 1.8	12.4	19.4	14.4 ± 0.7	4.9	34.0
G-4	25	91.8 ± 0.2	1.2	1.3	55.3 ± 3.4	16.5	29.8	58.3 ± 2.3	11.1	19.0	12.0 ± 0.6	2.9	24.1

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
G-5	18	90.8 ± 0.4	1.5	1.7	50.8 ± 3.3	13.8	27.2	80.1 ± 4.9	20.3	25.3	15.4 ± 1.1	4.5	29.2
G-6	6	90.1 ± 1.5	3.3	3.7	52.0 ± 5.5	12.3	23.7	69.3 ± 6.9	15.5	22.4	12.0 ± 1.5	3.4	28.3
G-7	11	89.4 ± 1.2	4.2	4.7	61.7 ± 6.7	21.1	34.2	80.9 ± 4.8	15.3	18.9	17.1 ± 1.8	5.6	32.7
G-8	11	88.5 ± 0.5	1.6	1.9	89.1 ± 6.1	19.3	21.7	90.6 ± 4.4	14.0	15.5	20.2 ± 1.5	4.8	23.8
G-9	22	87.7 ± 0.5	2.2	2.5	92.9 ± 3.7	16.8	18.1	82.5 ± 3.5	16.2	19.6	18.9 ± 1.2	5.8	30.7
G-10	12	85.9 ± 0.3	0.9	1.0	100.5 ± 1.7	5.5	5.5	84.4 ± 4.0	13.2	15.6	19.9 ± 1.2	3.9	19.6
G-11	12	85.7 ± 0.6	2.1	2.4	111.1 ± 2.0	6.6	5.0	76.1 ± 4.8	16.0	21.0	17.2 ± 1.5	5.0	29.1
G-12	19	85.3 ± 0.4	1.8	2.1	111.2 ± 1.5	6.3	5.7	64.2 ± 2.4	10.1	15.7	12.8 ± 1.0	3.1	24.2
G-13	8	85.2 ± 0.4	1.0	1.2	102.6 ± 4.5	12.0	11.7	67.4 ± 4.8	12.6	18.7	11.5 ± 1.3	3.7	32.2
G-14	1	86.0			102.0			58.0			10.0		
G-18	1	84.5			86.5			43.0			6.0		
G-19	2	87.0			68.8			63.0			7.5		
G-20	8	86.2 ± 0.4	1.1	1.3	83.6 ± 7.3	19.4	23.2	64.4 ± 5.9	15.6	24.2	8.4 ± 0.8	2.1	25.0
H-4	17	90.4 ± 0.3	1.3	1.4	57.4 ± 5.2	20.9	36.4	67.5 ± 2.8	11.2	16.6	13.6 ± 1.5	6.0	44.1
H-5	22	90.8 ± 0.4	1.7	1.9	54.1 ± 4.6	21.1	39.0	69.3 ± 3.0	13.7	19.8	12.8 ± 0.8	3.7	28.9
H-6	65	90.9 ± 0.2	1.3	1.4	52.6 ± 2.3	18.6	35.4	73.1 ± 1.7	13.4	18.3	15.3 ± 0.6	4.5	29.4
H-7	29	90.1 ± 0.3	1.6	1.8	49.6 ± 2.9	15.6	31.4	73.0 ± 2.3	12.3	16.8	16.5 ± 1.0	5.4	32.7
H-8	16	89.5 ± 0.7	2.7	3.0	58.2 ± 6.9	26.8	46.0	82.3 ± 4.6	17.8	21.6	16.1 ± 1.1	4.1	25.5
H-9	12	87.9 ± 0.8	2.6	3.0	77.3 ± 6.5	21.5	27.8	77.6 ± 4.4	14.5	18.2	18.6 ± 1.6	5.4	29.0
H-10	3	88.5			78.3			66.0			11.7		
H-11	17	85.6 ± 0.3	2.1	2.4	100.9 ± 1.9	13.1	12.0	69.4 ± 1.9	7.6	10.9	17.0 ± 1.2	4.6	27.1
H-12	26	85.4 ± 0.4	1.7	2.0	108.9 ± 2.0	9.8	9.0	70.2 ± 2.5	12.5	17.8	14.2 ± 0.9	4.4	31.0
H-13	38	84.8 ± 0.3	1.8	2.1	105.2 ± 1.6	9.8	9.3	64.5 ± 1.7	10.1	15.7	13.7 ± 0.7	4.3	31.4
H-14	16	84.2 ± 0.5	1.8	2.1	98.5 ± 2.9	11.4	11.6	63.4 ± 2.8	11.0	17.4	13.2 ± 0.8	3.2	24.2
H-15	2	81.5			112.0			69.0			16.0		
H-16	3	86.0			83.5			59.0			10.0		
H-17	3	87.0			86.0			57.7			6.7		
H-18	8	85.2 ± 0.8	2.1	2.5	88.1 ± 6.4	17.1	19.4	70.9 ± 2.7	7.1	10.0	11.9 ± 1.2	3.1	26.9
H-19	6	86.6 ± 0.4	0.8	0.9	87.5 ± 9.7	21.7	24.8	59.5 ± 5.8	13.1	18.6	7.0 ± 0.6	1.3	18.6
H-20	11	86.1 ± 0.5	1.7	2.0	83.8 ± 5.5	17.4	20.7	62.5 ± 3.6	11.3	18.1	8.3 ± 0.7	2.1	25.3
H-21	4	86.8			98.5			59.8			6.0		

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
I-4	27	91.4 ± 0.2	1.2	1.3	47.7 ± 3.4	17.5	36.7	62.3 ± 2.8	14.4	23.1	12.1 ± 0.7	3.4	28.1
I-5	7	90.9 ± 0.6	1.5	1.6	47.6 ± 8.6	21.0	44.1	64.4 ± 9.0	22.0	34.1	9.7 ± 1.5	3.7	38.1
I-6	28	90.9 ± 0.3	1.4	1.5	50.6 ± 3.8	19.7	38.9	65.2 ± 2.3	11.8	18.1	14.5 ± 1.1	5.5	37.9
I-7	26	91.2 ± 0.4	2.1	2.3	49.5 ± 3.5	17.3	34.9	63.1 ± 1.8	8.9	14.1	14.9 ± 0.8	4.1	27.5
I-8	10	89.6 ± 0.5	1.6	1.8	63.0 ± 5.3	16.0	25.4	66.7 ± 2.6	7.8	11.7	16.1 ± 1.9	5.6	34.8
I-9	10	88.2 ± 0.6	1.9	2.2	83.9 ± 8.7	26.0	31.0	67.8 ± 6.9	20.7	30.5	14.2 ± 1.5	4.4	30.9
I-10	19	87.8 ± 0.6	2.4	2.7	92.4 ± 5.3	22.4	24.2	78.7 ± 3.9	16.7	21.2	14.2 ± 0.9	3.9	27.5
I-11	31	86.9 ± 0.4	2.0	2.3	99.5 ± 3.2	17.6	17.7	71.8 ± 2.8	15.3	21.3	13.6 ± 0.9	5.0	36.8
I-12	17	86.5 ± 0.4	1.7	2.0	99.4 ± 3.8	15.1	15.2	68.8 ± 3.3	13.2	19.2	11.5 ± 0.8	3.3	28.7
I-13	62	85.1 ± 0.2	1.6	1.9	108.4 ± 1.3	9.8	9.0	63.7 ± 1.2	9.6	15.1	13.1 ± 0.4	3.4	25.9
I-14	14	84.6 ± 0.5	1.7	2.0	105.9 ± 2.0	7.3	6.9	65.3 ± 2.9	10.5	16.1	13.5 ± 0.9	3.2	23.7
I-15	2	85.2			102.7			52.5			14.0		
I-17	8	85.8 ± 0.8	2.1	2.4	84.9 ± 6.1	16.0	18.9	58.9 ± 3.4	8.9	15.1	10.0 ± 1.2	3.1	31.0
I-18	8	87.2 ± 0.4	1.0	1.1	71.0 ± 4.1	10.8	15.2	67.5 ± 5.1	13.4	18.4	7.9 ± 0.8	2.2	27.8
I-19	8	86.5 ± 0.4	1.2	1.4	82.3 ± 5.3	13.9	16.8	63.5 ± 4.8	12.8	20.2	7.5 ± 1.0	2.7	36.0
I-20	7	86.6 ± 0.4	1.1	1.3	79.6 ± 5.2	12.7	16.0	65.6 ± 5.3	12.9	19.7	8.3 ± 0.5	1.2	14.4
I-21	4	87.0			80.7			65.0			8.2		
J-5	10	91.3 ± 0.6	1.8	2.0	49.6 ± 6.5	19.6	39.5	61.0 ± 6.5	10.9	17.9	11.6 ± 1.6	5.2	44.8
J-6	2	90.8			65.8			46.0			10.0		
J-7	21	91.1 ± 0.5	2.3	2.5	47.6 ± 5.3	23.9	50.2	58.2 ± 1.4	6.5	11.2	10.8 ± 0.6	2.7	25.0
J-8	2	87.8			82.8			81.0			18.0		
J-9	12	89.4 ± 0.4	1.2	1.3	80.8 ± 4.9	16.2	20.0	56.5 ± 3.0	10.1	17.9	11.1 ± 0.9	3.0	27.0
J-10	9	88.9 ± 0.7	2.1	2.4	86.4 ± 5.8	16.4	19.0	64.1 ± 2.4	6.9	10.8	15.2 ± 1.1	3.0	19.7
J-11	8	87.8 ± 0.7	1.9	2.2	73.6 ± 10.6	28.0	38.0	62.6 ± 4.5	10.7	17.1	10.6 ± 1.4	3.6	33.9
J-12	14	87.1 ± 0.3	1.1	1.3	86.4 ± 4.4	16.0	18.4	62.4 ± 4.0	14.3	22.9	12.4 ± 0.8	3.0	24.2
J-13	34	85.5 ± 0.3	2.0	2.3	94.1 ± 3.1	17.7	18.8	64.0 ± 1.6	9.0	14.1	12.7 ± 0.6	3.3	25.9
J-14	7	84.5 ± 1.1	2.6	3.1	84.1 ± 9.4	22.9	27.2	56.4 ± 6.3	15.4	27.3	12.0 ± 1.6	3.9	32.5
J-17	13	85.7 ± 0.5	1.7	2.0	83.9 ± 6.2	19.6	23.4	65.5 ± 5.0	15.9	24.3	10.5 ± 1.1	3.6	34.3
J-18	11	86.6 ± 0.4	1.2	1.4	87.7 ± 4.0	12.6	16.6	72.0 ± 5.7	18.1	25.1	8.8 ± 0.8	2.6	29.5
J-19	26	87.0 ± 0.3	1.4	1.6	79.4 ± 3.3	16.6	20.9	69.0 ± 3.7	18.6	26.9	8.2 ± 0.5	2.4	29.3
J-20	3	87.3			64.0			75.7			12.0		

TABLE III *(Continued)*

Quadrat	N	∠A			∠B			Length			Width		
		$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
K-5	1	92.5			71.5			48.0			8.0		
K-6	1	91.5			53.0			60.0			10.0		
K-7	1	92.0			53.0			85.0			14.0		
K-8	3	90.7			65.3			65.0			12.3		
K-9	11	90.0 ± 0.4	1.4	1.6	69.1 ± 7.4	23.5	34.0	76.3 ± 5.8	18.4	24.1	13.2 ± 1.0	3.3	25.0
K-10	1	85.0			111.0			77.0			23.0		
K-11	11	88.7 ± 0.8	2.6	2.9	58.8 ± 6.2	19.5	33.2	58.1 ± 2.4	7.7	13.3	10.4 ± 0.9	2.8	26.9
K-12	18	87.6 ± 0.3	1.3	1.5	77.5 ± 4.3	17.6	22.7	58.6 ± 3.1	12.7	21.7	9.7 ± 0.6	2.6	26.9
K-13	13	87.5 ± 0.6	2.1	2.4	83.5 ± 5.7	19.6	23.5	54.5 ± 1.5	5.7	10.5	10.1 ± 0.5	1.8	17.8
K-14	1	86.5			106.0			75.0			18.0		
K-17	11	86.1 ± 0.5	1.6	1.8	79.4 ± 4.9	15.6	19.6	78.7 ± 0.4	14.2	18.0	12.3 ± 1.4	4.6	37.3
K-19	1	88.0			50.0			48.0			10.0		
K-20	4	86.9			86.1			59.7			6.0		
L-10	1	84.5			103.0			66.0			12.0		
L-12	11	87.3 ± 0.3	1.4	1.6	90.4 ± 3.8	11.9	13.2	54.6 ± 3.8	11.7	21.4	9.7 ± 1.2	3.7	38.2
L-13	27	87.2 ± 0.3	1.5	1.7	87.9 ± 4.6	23.4	26.6	54.3 ± 2.2	11.3	20.8	9.0 ± 0.6	2.9	31.1
L-14	7	86.1 ± 1.3	3.2	3.7	78.2 ± 6.1	14.8	18.9	50.0 ± 4.4	10.7	21.4	11.4 ± 1.6	4.0	35.1
M-16	1	87.5			46.0			51.0			6.0		
N-14	6	86.4 ± 1.0	2.3	2.6	68.8 ± 11.1	25.8	37.5	68.3 ± 6.5	14.5	21.2	7.0 ± 0.4	1.0	14.3

gression with the eastern subspecies. I consider the northeastern limit of "true" ssp. *interior* to approximate the converse of the northwestern limit of "true" ssp. *tuberosa*.

Attention has been called to the abrupt change of gradient of the genocline at approximately the middle. A paleogeographic explanation for this is seen in the fact that this location also approximates the southern terminus of the Pleistocene ice. North of this point, upon retreat of the ice, unusual opportunity for rapid migration must have been offered herbaceous plants with effective means of dissemination, such as milkweed with its comose seeds. Surely an unparalleled "open community" must have been offered them. Furthermore, the southern half of this cline traverses low, generally alluvial land unsuited to the species, where colonies are unusually sparse.

To this we must add obvious geographic features such as the more favorable climatic and edaphic conditions roughly north of this point. These factors apparently combine to explain why *Asclepias tuberosa* colonies of both subspecies are larger and more frequent roughly in the northern half of their ranges, as I have observed repeatedly. It is reasonable to expect more rapid gene flow, and consequently a more gradual cline, under such conditions than under those toward the south where the colonies are smaller and more widely separated.

Although the isophenes follow satisfactorily consistent courses, it is clear that both the individual quadrat means and their standard deviations would represent more or less distinctive population parameters within the broad intervals indicated. This also will be found true, but with different patterns, with regard to the other characters measured, as succeeding maps will show. Each quadrat population has its unique cell-like facets of mean tendencies and variabilities; all mutually dependent upon the constitution of their neighbor populations, but reflecting different internal forces. This heterogeneity within continuity will be found upon a lower level, but even more strikingly, in the account of natural populations which will follow.

The effects of introgression, therefore, are superimposed upon kaleidoscopic population patterns previously established by intra-subspecific gene flow in addition to diverse degrees of genetic drift; the latter, we may surmise roughly in inverse proportion to the former. I am inclined to discount any direct environmental effect on the expression of the two angular measures; but climatic and edaphic influence surely is exerted indirectly in moulding population tendencies in so far as it affects population size and frequency with regard to efficacy of gene flow, introgressive and otherwise.

The roles of population size and frequency in moulding population tendencies will be examined in more detail in another section of this paper. A preliminary intimation of their importance will be received upon examination in more detail of the quadrat statistics within the distribution of "true" *A. t. interior*, as indicated

by the map. In the Ozark region, where the subspecies is sufficiently frequent to be a roadside plant, the quadrat means for ∠A approximate a declination of 85.5°. The diminishing magnitude of the means as they progress toward the west suggests some slight, but diminishing, introgressive effect inadequately conveyed by the arbitrary isophene.

Near the boundary of the short-grass plains, population frequency drops abruptly, and the species ceases to be encountered commonly along roadsides. From this point some miles westward, one encounters a north-south distribution of plants with somewhat more sharply tapered leaves. As it happens, this tendency is associated with somewhat reduced length and somewhat increased width, so that a fairly recognizable race results.

In the high plains, the subspecies is absent or so rare that adequate quadrat samples are not available. In the better-watered highlands of New Mexico and Arizona it reemerges, however, but with such increased quadrat means that an effective mimicry of the introgressive populations of the Mississippi valley is obtained. Here also associated changes in other characters, especially greatly reduced width, produce something of a distinct racial facies.

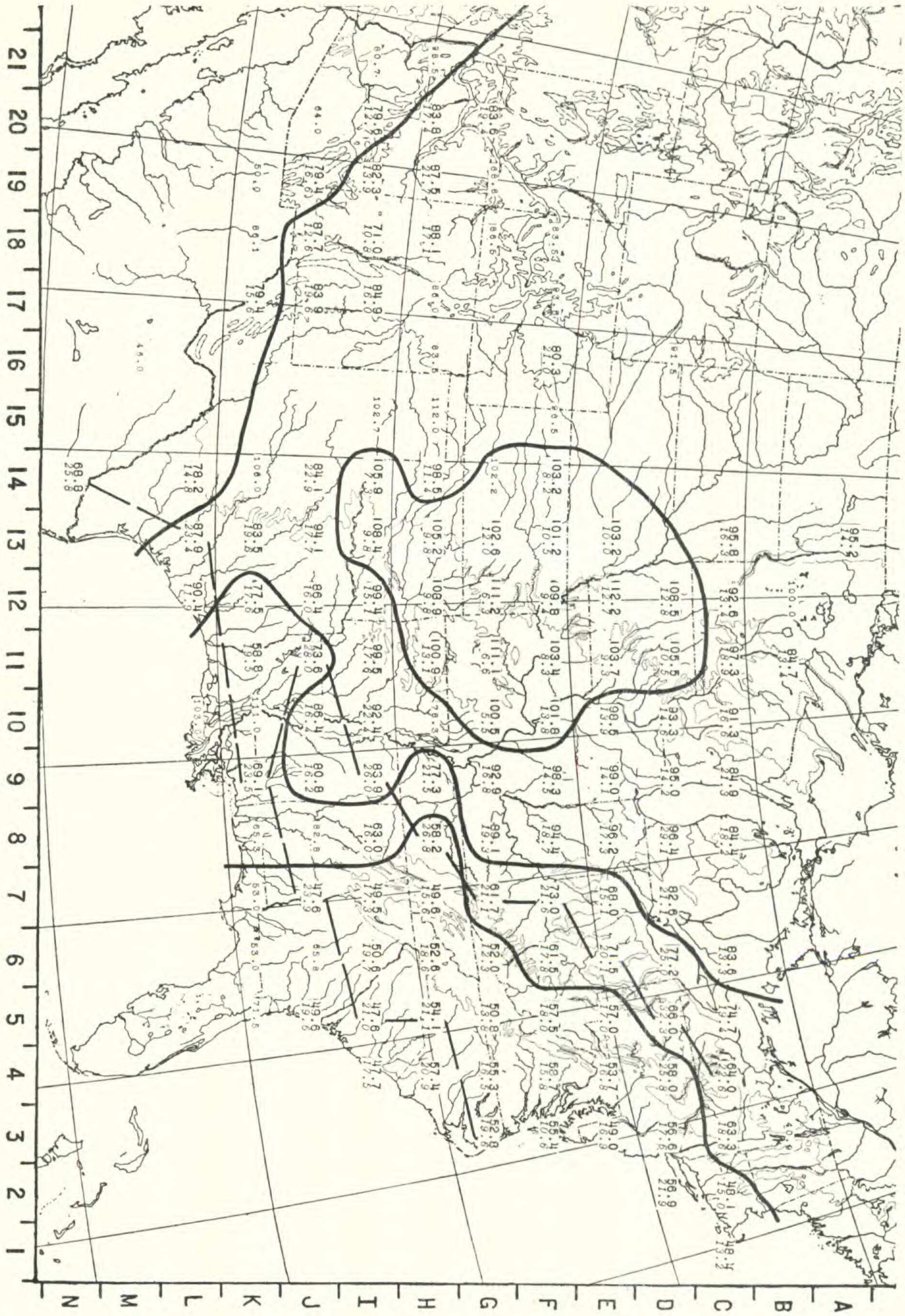
∠B

The phenocontour chart for ∠B, reproduced as Map IV, presents quadrat statistics in the same manner as did that for ∠A, but in this case isophenes have been drawn at intervals of 20° from the eastern seaboard. This interval was chosen after a hasty examination showed it to be the smallest which would produce continuous contours; hence it was surprising as well as gratifying when three isophenes emerged, separating four contours as in the preceding map. Here also the ranges of "true" *A. t. tuberosa* and "true" *A. t. interior* have much the previous relation to the Appalachian and Ozark plateaus, respectively, and the middle isophene denoting the midcurrent of introgression has somewhat the same course.

Dissimilarities to the ∠A map are striking, nevertheless. The isophenes themselves are more irregular and somewhat closer together, denoting a steeper cline. The eastern isophene, limiting the range of "true" ssp. *tuberosa*, has a more abrupt course to the Gulf coast, the reason for which will become apparent.

The phenocontours of ssp. *interior* are rather more complex than for ∠A, and show intra-subspecific differentiation in ∠B to be greater than in the former character. A far southwestern isophene is discovered here as well. Fortunately, confusion with the introgressive middle isophene is avoided here, since the two are not continuous. The most striking feature, however, is the irregularly elliptic 100°–110° contour eccentric in a northeasterly direction from the Ozark plateau.

The middle, introgressive, isophene is regular in the northern, glaciated states, and follows a course precisely similar to that seen in the map for ∠A. The southern half, however, is very irregular, showing three extensive and opposed embayments. Before interpreting these irregularities, we may observe that they



Map IV. *Asclepias tuberosa*: phenocontour system of ∠B (leaf base). Explanation in the text.

are the cause of the peculiarities of the ranges of the "true" subspecies already noted: the eccentricity of the 100°–110° contour of ssp. *interior*, and the abrupt course to the Gulf of the delimiting isophene of "true" ssp. *tuberosa*, or possibly the reverse is a more defensible position. At any rate, the evidence is mutually corroborative.

I would interpret the anomalous "bays" of the middle isophene as possibly connected with ecological, or at least floristic, selection. The Gulf coast embayment of the 60°–70° contour is a striking duplicate of typical southeastern coastal plain distributional extensions with which every plant geographer is thoroughly familiar. I believe that *A. t. Rolfsii* is implicated rather than *A. t. tuberosa* in this instance, because of the different characters of their distribution. Having been forced to omit the typical Floridian population from statistical analysis, this and another phenomenon to be presented shortly constitute our only evidence of the role of *Rolfsii* in introgression with the other subspecies.

The eastward embayment of the 80°–90° contour is typical, if less familiar, of the western floristic affinities of the isolated prairies of the middle-lower Mississippi valley (cf. Anderson & Woodson, 1935, in regard to *Tradescantia occidentalis* in eastern Arkansas). The third and northernmost embayment westward probably testifies to the Appalachian affinity of the area about the Nashville basin. The conclusion to be drawn from the embayments possibly is that in some way these floristic regions are peculiarly conducive to either subspecies as the case may be, and that in some way the factors for leaf base are correlated with others governing ecological adaptability of the subspecies in a manner not affecting leaf taper. With data as fragmentary as it is, the differential gene flow for the characters ∠A and ∠B in this region nonetheless appears obvious.

In discussing the map for ∠A, attention was called to the distinctive statistical facies of the quadrat populations. The same heterogeneity within continuity is found to obtain with regard to ∠B, although here it assumes more significant proportions. Attention was directed in the earlier discussion to the southwestern diversification of *A. t. interior*. Something of the same phenomenon is seen to involve ∠B. Here, intra-subspecific differentiation produces an irregularly centrifugal lowering of the quadrat ∠B means, i. e., a tendency for the leaves to become progressively less cordate. This phenomenon, together with others associated with it, will be examined more closely in another section of this study.

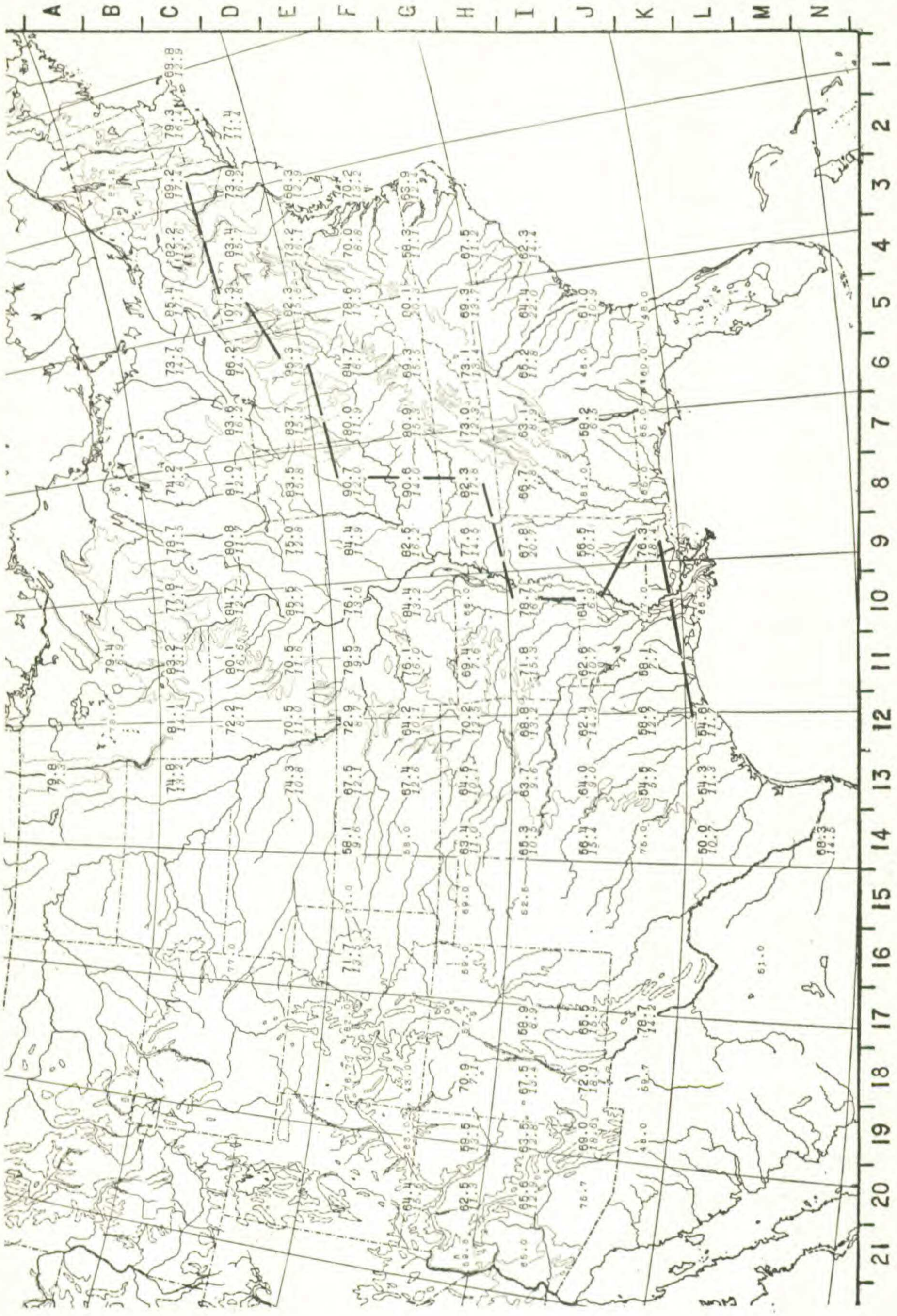
Perhaps the most striking feature of Map IV is the two convergent series of broken lines. These lines were drawn connecting quadrats having the greatest standard deviations when it was discovered that the deviations for ∠B means, unlike those for ∠A means, appear to have a more or less defined contour system of their own. The series of broken lines from central New York to Texas was drawn first, connecting the highest deviations in each horizontal rank of statistics. After this was completed, I observed that a similar, almost parallel, contour to the southeast could be obtained by connecting the deviations next in size.

As far as I am aware, this type of introgressive contour has not been discussed previously, and has not been provided with a name. I shall call it merely the "crest of variability" until I am inspired by appropriate classical roots. At any rate, involved with physiographic allegory as we are, it is natural to think of these crests of variability of ∠B as being due to a kind of genetic orogeny produced by introgression pressure from the three subspecies. This interpretation is supported by the obvious fact that the longer crest follows the 60°–70° contour between *A. t. tuberosa* and *A. t. interior* quite closely, and that the shorter crest to the southeast approximates the commissure of *A. t. tuberosa* and *A. t. Rolfsii* in almost exactly the position that any plant geographer would predict.

It would appear remarkable indeed if the longer crest of variability were to parallel more exactly the middle isophene throughout its devious southern course. Two explanations of its rather minor unconformity suggest themselves: one statistical, the other biological. The first concerns the strategic population in central Alabama which unfortunately contains too few cases for the computation of standard deviation. Were this statistic sufficiently large, the crest of variability would pass through it and successfully negotiate the sharp turn into coastal Texas in perfect harmony with the sinuous contour. The second explanation is less trifling: the fact that any increased variability due to heterozygosis must be superimposed upon the pre-existing parameter variability of each quadrat, the range of which may be seen by observing the heterogeneity of deviations in areas not possibly affected by introgression. The intriguing fact, therefore, is that the crest is as consistent as it is.

The relatively close conformity of the longer crest of variability with the 60°–70° contour leads me to conclude that introgression is progressing more rapidly from west to east, and threatens to engulf the Appalachian population. Evidence that *Rolfsii* is advancing in similar fashion will be deduced later. Caught between the advances of its sister subspecies upon either side, the ultimate reduction of ssp. *tuberosa* to a hybrid swarm would appear unavoidable. Some indications of the rate and manner in which this is being accomplished will follow shortly.

That no crest of variability was produced on the map for ∠A, such as that which we have just seen with regard to ∠B, appears of fundamental importance to me. I am led to the conclusion that very different gene actions must be responsible for the expression of the two characters. According to the theory of oligogenes and polygenes (Mather, 1942), one might expect such a crest of variability in introgressions involving the former and not the latter. The great difficulty in applying this theory to our phenocontour data is the lack of knowledge concerning the hereditary mechanism governing the characters measured. This is scarcely surprising since the plants do not lend themselves easily to breeding experiments, and further because both characters of leaf shape may be presumed to be controlled by multiple factors. A consequent difficulty for me is uncer-



Map V. *Asclepias tuberosa*: phenocontour system of median length of leaves. Explanation in the text.

tainty whether one should regard oligogenes and polygenes as allowing an ample continuous scale of graded expression; in other words, how many genes may constitute an oligogene complex, and how few a polygene, or is the distinction a relative one?

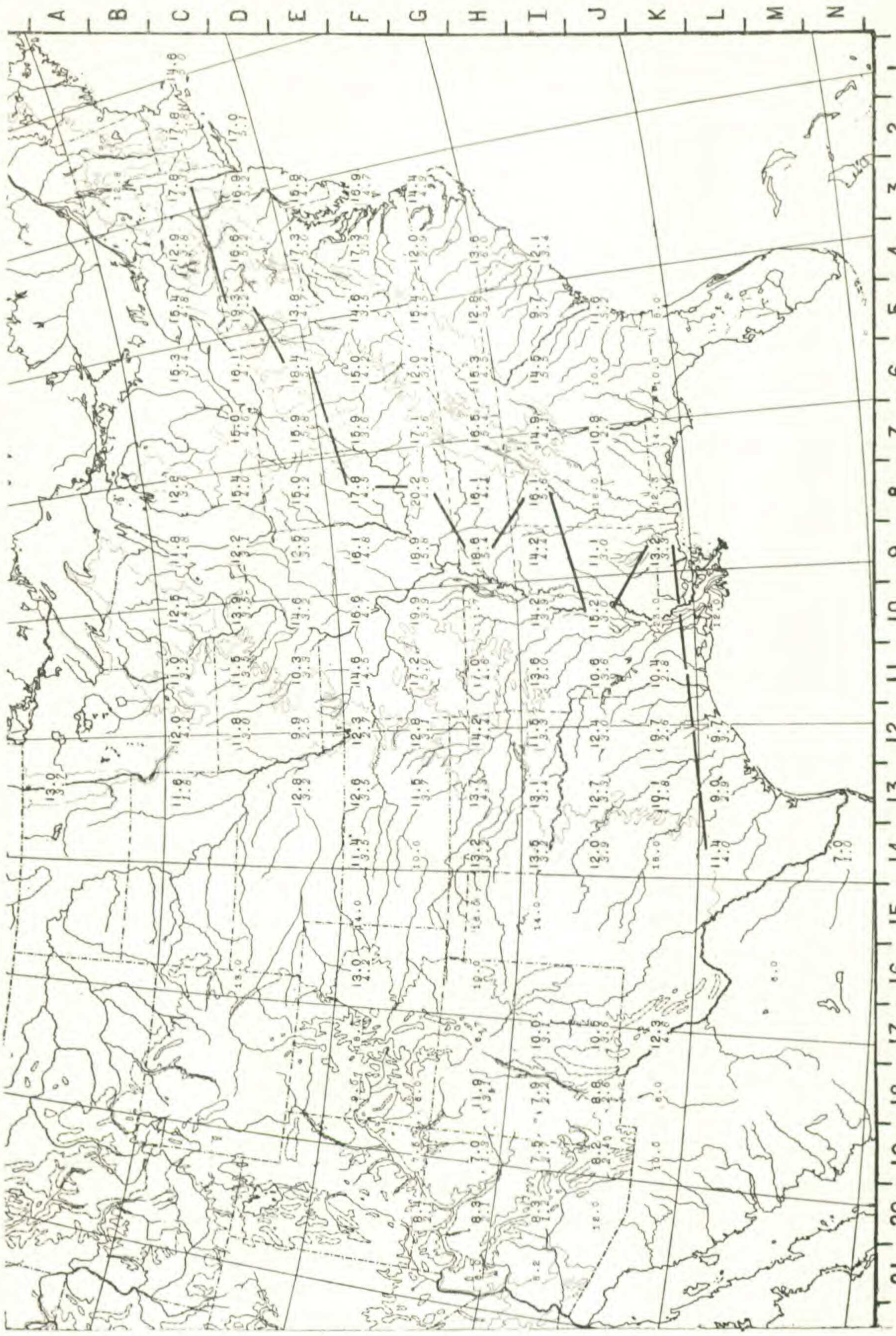
LENGTH AND WIDTH

The phenocontours of median length (Map V) and median width (Map VI) may be discussed together since they show much the same characteristics. In both maps the same tendency of quadrat populations to drift about individual means and variabilities is seen, as has been noted in connection with the other characters. In the maps for length and width, however, it is not practicable to draw isophenes, since these characters are not involved in the differentiation of the subspecies. In Map V an irregular tendency may be noted for leaves of both subspecies to be somewhat longer in the north than in the south. In Map VI the leaves of *A. t. interior* are found to be narrowest in the extreme southwest of the range. It seems most probable that these tendencies are produced in response to climate, from what we have learned of the relative frequency of the subspecies in different parts of its range; the result is a series of rather poorly defined ecoclines.

The most prominent feature of both maps is the oblique series of broken lines extending from New York state to coastal Texas. These lines, in both instances, connect the largest mean in each horizontal rank of quadrats, with the exclusion of the far southwestern quadrats of Map V. The two courses of broken lines are almost identical, diverging in respect to only two pairs of quadrats. It is apparent also that they approximate very closely the crest of variability observed with regard to $\angle$B, even to the peculiar switch-back on the Gulf coast.

I cannot conceive, upon the evidence of the three maps, that the courses of broken lines for length and width can indicate other than hybrid vigor. Environmental effect can be discounted apparently because the lines run contrary to the ecocline contours for length. The combination of the two effects may be seen in both maps in that there is a general tendency for the maximum means to decrease from north to south. Of further interest is the indication that heterosis, if such it be, has little effect upon the variability of the populations with regard to length and width. These two properties would indicate that heterosis in natural populations, like the crest of variability previously discussed, is a quality superimposed upon previously established quadrate parameters. Heterosis cannot be regarded as greater in the northern states, and therefore that those populations are more heterozygous, simply because the northern maxima are greater than are those in the south. Northern leaves, *in general*, are larger than those in the south. This explains why the crests of length and width maxima do not correspond exactly, and, I am confident, why they do not correspond exactly with the crest of variability.

Several genetical problems of importance arise in reply to the interpretations which have just been made. Since a crest of variability was observed between the



Map VI. *Asclepias tuberosa*: phenocontour system of median width of leaves. Explanation in the text.

ranges of ssp. *tuberosa* and ssp. *Rolfsii*, why is there no parallel heterosis similar to that involving *tuberosa* and *interior?* One might suppose that the differences distinguishing the former two were insufficient to produce the necessary relational genic disbalance. From the purely systematic point of view, there can be little doubt that *tuberosa* and *Rolfsii* are more closely related than is either to *interior*. The difference between the two former, however, still must be sufficient to produce the crest of variability.

It is conceivable that *tuberosa* and *interior* have been in direct contact only since colonial times, due to the clearing of land, the building of roads, etc., although we can scarcely be sure of this. Even so, how has heterosis been maintained to the present day? Only by continuous gene flow from inbred populations, we may expect. Of importance in this regard, probably, are the air-borne seeds and peculiar adaptations to insect pollination described in the earlier portion of this paper.

Heterosis, according to Mather (1943) and others, results from the bringing together of polygenic combinations which have not been selected for good relational balance, and because of this, the phenotype of the hybrid will be likely to show a greater departure from the optimum than does either parent. It follows that heterosis is a sure sign of poor adaptation, and must be selectively disadvantageous and less "fit" than the parental types. In this way, it is believed, isolating mechanisms and hybrid sterility originate; indeed, "the avoidance of heterosis is the most widespread stimulant of isolating devices."

Certainly it would be unbecoming of me to enter into a controversy of genetical theory. In my opinion, however, there is a tendency to ascribe too uniform selective value to indiscriminate types of biological variations. Until a correlated character involving some aspect of viability or physiological efficiency is discovered, I can attach little selective advantage to any of the types of leaves which I have measured. I am convinced that plants of the inclusive species *Asclepias tuberosa* are nowhere as frequent, as fertile, nor as happily adapted to their environment as in the zig-zag commissure between the subspecies *tuberosa* and *interior*, where they apparently are most heterozygous.

With gradual discontinuance of out-breeding to "pure" types, I would expect relative subsidence of both excessive variability and heterosis, and a genetic peneplanation to a poorly differentiated hybrid swarm—the raw material of future speciation. In the light of our introductory discussion of paleogeography, I can see no reason why this has not occurred, perhaps repeatedly, in the past. A primary function of introgression may be the imparting of greater variability to specialized parental stocks. My experience in the field with the apparently successful establishment of introgressive populations of *A. tuberosa* prompts me to disbelieve that heterosis alone will lead to the erection of isolating devices to reseparate the subspecies. As a matter of fact, the following section of this study will produce evidence that introgression between *A. t. tuberosa*, *A. t. interior*, and *A. t. Rolfsii* is continuing apace.

V. ANALYSIS OF A ROADSIDE PROFILE

In June, 1946, I made an automobile trip from Topeka, Kansas, to Norfolk, Virginia, accompanied by two of my friends, Richard W. Holm and George K. Richardson. The purpose of the journey was to collect leaves of butterflyweed from every colony of five or more plants encountered between those two points, for comparison with the herbarium data from a similar profile. The route chosen followed U. S. highway 40 eastward to St. Louis, U. S. 50 and 150 to Louisville, and U. S. 60 to Norfolk. The final collection, as a matter of fact, was made at Chuckatuck, Virginia, a village on U. S. highway 17, a few miles south of Norfolk. The whole transect totals a distance of about 1200 miles.

The massive plants and broad trusses of brilliant flowers render *Asclepias tuberosa* a conspicuous object from a distance of many yards, even when surrounded by undergrowth equalling or exceeding its height. Cruising at a speed averaging approximately 40 m. p. h., my companions and I had no difficulty whatsoever in detecting the species, I should guess, from a distance averaging at least one-tenth mile along either side of the highway. With three pairs of eyes vying for the first welcome sight of orange, I fancy that few plants escaped us.

With the cry of "Butterflyweed!", brakes would scream and out we we would spring to see whether the find consisted of a single plant or two, which we would neglect, or a colony of at least five. If the colony proved to be a large one, all hands would set to work, quickly selecting a portion for exclusive attention, and nimbly divesting one flowering stem of each plant of a single "random" median leaf. Back in the car, the leaves would be united into a paper envelope inscribed with appropriate data, inserted into a press, and probably sat upon by Dick, George, or myself. Perhaps more important biometric material has been secured within four days, and from a wider area, but never more happily.

The transect which has just been described yielded a total of 994 leaves for measurement; these were distributed amongst 53 colonies of five plants or more. The largest colony numbered 77 plants; the median colony size for the whole transect was 13. Unfortunately, no record was kept of single plants encountered, nor of small colonies of less than five plants, but these certainly were met with far more seldom than the "larger" colonies; perhaps a total of 1050 plants were encountered in all.

The distance between colonies for which records were kept varied from 3 to 107 miles, with a median distance of 12 miles. Between these, of course, were interspersed the single plants and smaller colonies. The mean distance between colonies varied in a manner to which some degree of significance may be attached, the greatest concentration occurring in Kansas and Missouri (16–22 miles) on the western end, and Virginia (14 miles) on the eastern. The most sparse colonies were encountered in Illinois, where the mean distance was 46 miles. From such a small sampling, only a general inference may be made to the effect that the colonies

were more frequent the closer to the putative centers of origin of the two subspecies, an observation which I take to have more paleogeographic than genetical bearing.

As relief from more practical considerations, I have indulged in some conjecture concerning the total population of *Asclepias tuberosa* in the United States. From the details of the journey which have been given, it may be estimated crudely that a total area approximating 243.6 square miles was searched for butterflyweed, with an estimated total of 1050 plants, yielding a density approximately of 4.3 per square mile. Estimating the total area of the species as 1,434,000 square miles, a total population in excess of 6,000,000 plants is suggested. The unreliability of this figure is emphasized by the realization that the area actually sampled equals less than one-five thousandths of the estimated total area!

Similarly facile computations may be made concerning the potential fecundity of the species for comparison with the estimated frequency which has been observed. For our crude purposes, we may assume the potential fecundity of an "average" plant of butterflyweed to be the product of approximately 100 ovules distributed amongst 2 carpels for each of 18 flowers per cyme, with 15 cymes per stem. Assuming an average of 15 stems per plant, a potential seed crop of 405,000 seeds per plant is indicated, a figure which is no more disproportionate to actual population than is usual in such computations.

In the earlier discussion of the biology of the species, certain mechanical factors influencing the failure to realize this potential fecundity have been indicated, *i. e.*, difficulties of pollen transference and the division of the stigmatic surface into 5 separate areas. To these must be added the observed somatoplastic sterility and relatively low germination in nature, as well as the more enigmatic animal predators and rigors of ecological competition. Having by no means exhausted the possibilities, it is clear why plants are such satisfactory subjects for systematic and geographical studies: why they stay "close to home" as a rule; why they are conservative to evolutionary change. It also is clear why more precise genetic concepts are not forthcoming from studies such as these.

Table IV presents the individual statistics for the 53 colonies of butterflyweed encountered along the 1218-mile profile from Topeka, Kansas, to Chuckatuck, Virginia. In fig. 4 they are presented in the form of a composite graph, including the means and standard deviations for the four characters of ∠A, ∠B, median length, and median width. The abscissa of the graph indicates the proportionate distances of the colonies, the numbers corresponding to those employed in Table IV. The principal physiographic features encountered in the transect are indicated on the face of the graph between the data for length and width. Drawn to such a scale, the clines and other features noted in the phenocontour maps are scarcely recognizable in fig. 4, which to this degree approaches reality rather disconcertingly. Nevertheless, with a bit of scrutiny, the graphs may be found to corroborate satisfactorily the clines, as well as the crests of variability and hybrid vigor to which attention was called by the maps.

TABLE IV

MEASUREMENTS OF LEAVES OF *ASCLEPIAS TUBEROSA* (SENSU LAT.) ASSEMBLED ACCORDING TO NATURAL COLONIES ALONG ROADSIDES FROM TOPEKA, KANSAS, TO CHUCKATUCK, VIRGINIA

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
1	East of Topeka, Shawnee Co., Kans.	11	84.6 ± 0.6	2.0	2.4	106.3 ± 1.9	6.2	5.8	63.4 ± 2.8	8.8	13.9	12.4 ± 1.1	3.4	27.4
2	8 mi. east of Topeka, Shawnee Co., Kans.	10	85.0 ± 0.2	0.7	0.8	104.2 ± 2.8	8.5	8.1	67.2 ± 2.1	6.3	9.4	12.8 ± 0.4	1.3	10.1
3	West of Lawrence, Douglas Co., Kans.	15	84.5 ± 0.4	1.3	1.5	110.6 ± 2.4	8.9	8.0	72.3 ± 3.3	12.3	17.0	14.3 ± 1.9	4.1	28.6
4	Lawrence, Douglas Co., Kans.	33	84.7 ± 0.2	1.4	1.7	107.3 ± 1.2	6.6	6.2	73.2 ± 2.0	11.1	15.2	14.4 ± 0.6	3.3	22.9
5	10 mi. east of Lawrence, Douglas Co., Kans.	17	85.3 ± 0.2	1.7	1.8	107.5 ± 1.8	7.3	6.8	69.6 ± 2.8	11.2	16.1	14.1 ± 0.7	2.7	19.1
6	20 mi. east of Kansas City, Jackson Co., Mo.	10	86.0 ± 0.4	1.2	1.4	113.3 ± 1.6	4.7	4.1	71.9 ± 5.0	14.9	20.7	13.8 ± 0.5	1.6	11.6
7	East of Odessa, Lafayette Co., Mo.	10	87.0 ± 0.3	0.9	1.0	101.5 ± 2.4	7.3	7.2	79.3 ± 3.4	10.1	12.7	13.0 ± 2.5	2.8	21.5
8	6 mi. west of Concordia, Lafayette Co., Mo.	8	85.3 ± 0.5	1.2	1.4	99.6 ± 3.9	10.3	10.3	84.1 ± 3.9	10.2	12.1	14.6 ± 1.2	3.1	21.2
9	Southwest of Marshall, Saline Co., Mo.	7	85.8 ± 0.9	2.2	2.6	107.8 ± 5.8	17.8	22.0	81.0 ± 7.3	17.8	22.0	16.6 ± 2.1	5.1	30.7
10	East of Columbia, Boone Co., Mo.	11	85.9 ± 0.5	1.6	1.6	108.2 ± 3.7	11.6	10.5	87.2 ± 2.8	8.9	10.2	17.8 ± 1.2	3.9	21.9
11	2 mi. east of Kingdom City, Callaway Co., Mo.	5	85.8 ± 1.5	3.0	3.5	105.7 ± 4.1	8.2	7.8	76.2 ± 5.4	10.7	14.0	18.0 ± 2.6	5.2	28.9
12	4 mi. east of Kingdom City, Callaway Co., Mo.	17	85.9 ± 0.3	1.1	1.5	96.1 ± 2.2	8.8	9.2	85.2 ± 1.6	6.5	7.6	17.6 ± 1.1	4.2	23.5
13	Warren-Montgomery county line, Mo.	5	89.2 ± 1.1	2.1	2.4	85.5 ± 8.8	17.5	20.5	73.8 ± 4.6	9.1	12.3	13.0 ± 0.7	1.4	10.8
14	2 mi. east of Wright City, Warren Co., Mo.	11	87.3 ± 0.4	1.3	1.4	92.9 ± 3.9	12.4	13.4	73.9 ± 3.0	9.5	12.8	16.1 ± 1.5	4.6	28.6

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
15	Wentzville, St. Charles Co., Mo.	32	87.1 ± 0.2	0.9	1.0	97.7 ± 1.7	9.4	9.6	85.4 ± 2.6	14.6	17.1	15.9 ± 0.6	3.5	22.1
16	Glendale, St. Louis Co., Mo.	36	86.6 ± 0.3	1.5	1.7	97.3 ± 2.2	13.2	13.6	86.2 ± 2.1	12.1	14.0	18.1 ± 0.9	5.2	28.7
17	Edwardsville, Madison Co., Ill.	20	87.6 ± 0.2	1.0	1.1	108.4 ± 2.3	10.1	9.3	83.7 ± 1.1	5.0	5.9	15.6 ± 0.8	3.3	21.2
18	West of Trenton, Clinton Co., Ill.	8	87.1 ± 0.3	0.9	1.0	100.6 ± 3.0	8.0	7.9	80.4 ± 5.3	14.1	17.5	15.4 ± 0.6	1.7	11.0
19	East of Bridgport, Lawrence Co., Ill.	5	89.0 ± 0.8	1.6	1.8	92.1 ± 10.1	20.2	21.9	77.2 ± 2.1	8.4	10.9	14.4 ± 1.4	2.9	20.1
20	Washington, Daviess Co., Ind.	5	86.2 ± 1.2	2.4	2.8	96.5 ± 2.7	5.5	5.7	93.2 ± 5.0	10.0	10.7	21.4 ± 1.8	3.5	16.4
21	East of Washington, Daviess Co., Ind.	13	88.3 ± 0.4	1.5	1.7	89.2 ± 2.5	9.5	10.6	104.9 ± 4.6	15.9	15.2	21.4 ± 1.0	3.4	15.9
22	Southeast of Paoli, Orange Co., Ind.	77	89.1 ± 0.2	1.2	1.4	79.8 ± 1.8	16.0	20.0	92.5 ± 1.5	12.2	13.2	16.9 ± 0.4	3.4	20.1
23	East of Shelbyville, Shelby Co., Ky.	46	88.9 ± 0.2	1.5	1.7	75.0 ± 2.9	19.8	26.4	92.2 ± 1.9	12.6	13.7	20.6 ± 0.7	4.7	22.8
24	East of Owingsville, Bath Co., Ky.	17	89.6 ± 0.2	1.0	1.1	61.1 ± 4.5	18.0	29.5	93.4 ± 2.7	10.7	11.5	17.5 ± 0.6	2.6	14.9
25	Northeast of Morehead, Rowan Co., Ky.	6	89.1 ± 0.5	1.2	1.3	52.8 ± 4.4	9.8	18.6	99.0 ± 3.9	8.7	8.8	18.3 ± 1.5	3.4	18.6
26	Eadston, Rowan Co., Ky.	12	89.8 ± 0.4	1.2	1.3	68.0 ± 5.2	17.4	25.2	110.9 ± 3.7	12.2	11.0	15.1 ± 1.2	4.1	27.1
27	Grayson, Carter Co., Ky.	6	90.2 ± 0.4	0.8	0.9	49.6 ± 2.0	4.5	9.1	81.3 ± 11.6	26.1	32.1	12.8 ± 2.2	5.0	39.1
28	Jaffie, Lawrence Co., Ky.	5	89.0 ± 0.6	1.1	1.2	70.4 ± 3.4	6.7	9.5	103.2 ± 1.6	3.3	3.2	23.6 ± 1.9	3.9	14.8
29	East of Huntington, Cabell Co., W. Va.	8	90.0 ± 0.4	1.1	1.2	68.1 ± 6.7	17.8	26.2	97.9 ± 4.2	17.8	11.3	15.5 ± 1.2	3.3	21.3
30	Milton, Cabell Co., W. Va.	8	90.4 ± 0.4	1.1	1.2	47.6 ± 4.5	12.0	25.2	90.2 ± 4.5	12.0	13.3	15.3 ± 2.0	5.2	33.9

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
31	East of Milton, Cabell Co., W. Va.	11	87.8 ± 0.7	2.3	2.6	70.3 ± 5.8	18.2	25.9	103.7 ± 7.6	24.0	23.1	20.1 ± 1.3	4.0	19.9
32	Gauley's Mountain, Fayette Co., W. Va.	17	89.6 ± 0.4	1.6	1.8	55.6 ± 3.4	13.5	24.3	89.7 ± 3.4	13.8	15.4	14.0 ± 0.7	2.8	20.0
33	West of Covington, Allegheny Co., Va.	11	88.7 ± 0.4	1.5	1.7	67.7 ± 4.8	15.1	22.3	73.7 ± 2.7	8.7	11.8	16.8 ± 1.0	3.2	19.0
34	Covington, Allegheny Co., Va.	60	88.1 ± 0.2	1.8	2.0	70.3 ± 2.4	18.2	25.9	71.2 ± 1.8	13.7	19.2	16.7 ± 0.6	4.8	28.7
35	North Mountain, Rockbridge Co., Va.	67	89.1 ± 0.2	1.7	1.9	76.4 ± 2.2	17.7	23.2	85.3 ± 1.4	11.8	13.8	18.4 ± 0.6	5.2	28.3
36	North Mountain, Rockbridge Co., Va. (2nd colony)	21	89.4 ± 0.4	1.6	1.8	64.1 ± 3.7	16.6	25.9	75.9 ± 2.6	11.6	15.3	16.3 ± 1.2	5.2	31.9
37	East slope, North Mountain, Rockbridge Co., Va.	8	90.4 ± 0.7	1.8	2.0	68.3 ± 8.1	21.6	31.6	89.1 ± 5.5	14.4	16.2	15.8 ± 1.1	2.9	18.4
38	East of Lexington, Rockbridge Co., Va.	53	89.9 ± 0.2	1.4	1.6	70.0 ± 2.4	17.6	25.1	80.9 ± 1.7	12.4	15.3	19.9 ± 0.7	4.8	24.1
39	West of Amherst, Amherst Co., Va.	26	89.3 ± 0.4	2.1	2.4	63.9 ± 3.8	19.0	29.7	83.7 ± 2.8	14.1	16.8	23.3 ± 1.2	5.8	24.9
40	Bent Creek, Appomattox Co., Va.	6	88.8 ± 0.6	1.4	1.6	69.8 ± 4.3	9.5	13.6	88.8 ± 6.2	13.9	15.7	25.7 ± 1.9	4.2	16.3
41	Between Bent Creek and Buckingham, B'ham Co., Va.	14	89.9 ± 0.4	1.6	1.8	64.5 ± 5.1	18.3	28.4	67.8 ± 2.9	10.6	15.6	18.7 ± 2.0	7.2	38.5
42	Buckingham, Buckingham Co., Va.	34	90.5 ± 0.3	1.7	1.9	66.5 ± 2.8	15.8	23.8	72.7 ± 2.1	12.3	16.9	19.3 ± 0.8	4.0	20.7
43	8 mi. west of Cumberland, Cumberland Co., Va.	5	87.9 ± 1.8	3.6	4.3	64.9 ± 6.6	13.3	20.5	79.6 ± 6.8	13.7	17.2	22.2 ± 4.0	8.1	36.5
44	Northwest of Skinquarter, Powhatan Co., Va.	20	89.9 ± 0.4	1.6	1.8	71.8 ± 3.1	13.3	18.5	66.7 ± 2.9	12.4	18.6	17.0 ± 1.0	4.2	24.7
45	Midlothian, Chesterfield Co., Va.	15	90.7 ± 0.4	1.6	1.8	76.4 ± 3.4	12.8	16.8	63.4 ± 3.2	11.8	18.6	16.1 ± 1.0	3.8	23.6

TABLE IV *(Continued)*

No.	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
46	Providence Forge, New Kent Co., Va.	13	91.6 ± 0.6	2.0	2.2	61.5 ± 4.1	14.2	23.1	62.4 ± 3.1	10.7	17.1	14.2 ± 0.9	3.0	21.1
47	Providence Forge, New Kent Co., Va. (2nd colony)	7	88.7 ± 0.7	1.7	1.9	69.8 ± 7.2	17.7	25.4	65.3 ± 3.1	7.7	11.8	16.3 ± 1.3	3.3	20.2
48	Windsor Shades, New Kent Co., Va.	44	89.0 ± 0.3	2.2	2.5	74.1 ± 2.1	13.8	18.6	70.6 ± 1.8	11.6	16.4	19.1 ± 0.8	5.6	29.3
49	West of Toano, James City Co., Va.	17	90.1 ± 0.6	2.2	2.4	70.3 ± 3.5	13.9	19.8	66.8 ± 2.8	11.3	16.9	14.9 ± 0.9	3.7	24.8
50	Ewell, James City Co., Va.	6	89.6 ± 0.6	1.4	1.6	70.5 ± 6.1	13.5	19.1	68.2 ± 3.5	7.9	10.1	16.5 ± 1.8	4.0	24.3
51	Lee Hall, Warwick Co., Va.	20	91.6 ± 0.4	1.6	1.7	57.8 ± 4.4	19.0	32.9	69.2 ± 1.7	7.4	10.8	16.6 ± 0.8	3.3	19.9
52	Benn's Church, Isle of Wight Co., Va.	31	91.1 ± 0.3	1.4	1.5	56.4 ± 2.3	12.4	22.0	69.1 ± 2.2	12.2	17.7	18.5 ± 1.0	5.6	30.3
53	South of Chuckatuck, Nansemond Co., Va.	14	92.1 ± 0.4	1.2	1.3	54.5 ± 2.5	9.0	16.5	75.3 ± 3.2	11.4	15.1	14.7 ± 1.0	3.6	24.5

Aside from area, the first feature of the graph to catch the eye may be the relative smoothness of the curves for width, and particularly for ∠A, in contrast to those for ∠B and length. This is chiefly a statistical effect occasioned by the small total range of ∠A means, on the one hand, and the relatively small size of width means, on the other. If *V* had been used as a standard measure of variability instead of *s*, for example, the curve for width would have been the most irregular by far.

A more significant feature is seen in the increased irregularity of all curves from the Allegheny Mountains eastward to the coast. Since the profile traverses the central lowlands westward to the Alleghenies, an accounting factor for the conspicuous variability eastward might be advanced as the more varied topography *per se*. Considering the roadside origin of my samples, I am not impressed by this explanation. Another might be the assumption of greater intrinsic variability in colonies of *A. t. tuberosa* than in those of *A. t. interior*. This is not likely since certain colonies of the former on the Atlantic seaboard have quite as low variability as colonies of the latter on the midwestern plains.

I am disposed to view the regularity west of the Alleghenies and the irregularity to the east as being evidence of greater migration pressure of the western subspecies, producing greater heterozygosity, and hence variability, in the eastern population through introgression. I shall explore this possibility more fully in succeeding sections.

It is apparent that the colonies behave as microgeographic races, those immediately adjacent to one another often being more different, in a given character, than others a hundred or more miles away (cf. Anderson, 1936; Dice, 1940). Nevertheless, for all their haphazard courses, there are definite clines, both for ∠A and for ∠B. This composite effect presumably is the result of random fixation and loss of genes in colonies with limited effective population size (Dobzhansky, 1941), combined with the occasional exchange of genes between adjacent colonies. The latter, of course, is effected through insect agency in the final analysis, but doubtless is facilitated by the long-distance transport of seeds from either direction, particularly from west to east—the course of the prevailing winds.

In view of the relatively great distances between colonies, their relatively few individuals, and their distinctive parameters, I am of the opinion that such colonies are the progeny of a single plant germinating from a single wind-borne seed, as a rule; which in turn largely accounts for their distinctive facies. In consideration of the apparently facultative cross- or self-pollination, I assume the effective population size of butterflyweed to be low indeed.

A pair of little scatter diagrams which interest me specially are reproduced as figs. 5-6, since they do much to explain the genetic mechanism of introgression with regard to both ∠A and ∠B. In fig. 5, the dots represent the coincidence of the means of ∠A and ∠B obtained from each of the 53 colonies of butterflyweed

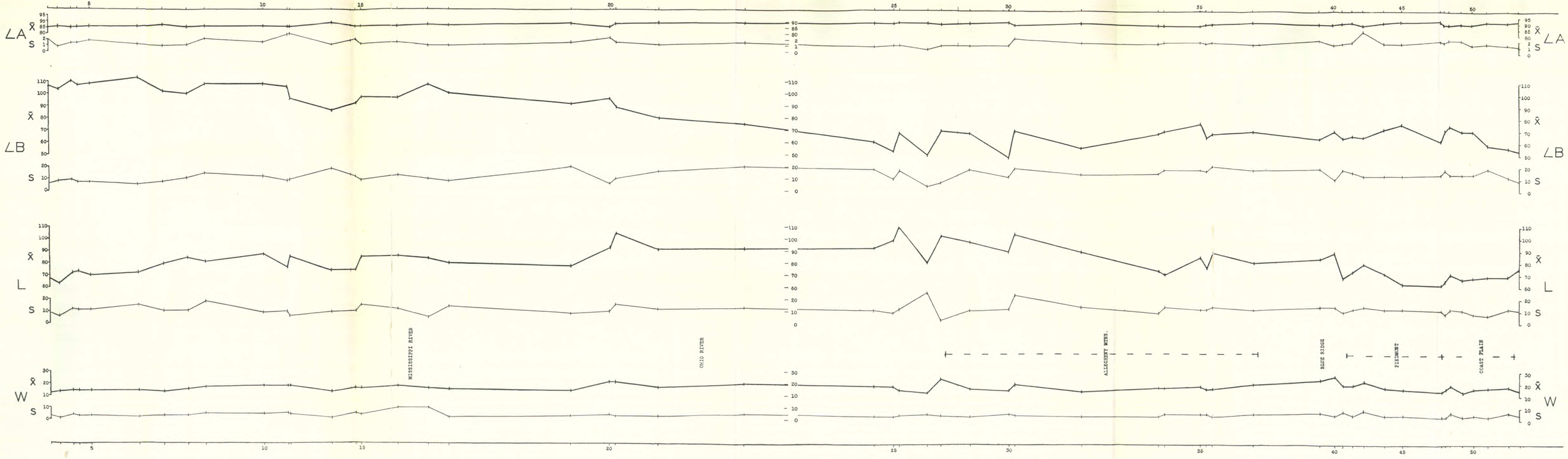


Fig. 4. Means and standard deviations of 53 colonies of butterflyweed along a roadside profile from eastern Kansas to Tidewater Virginia. Explanation in the text.

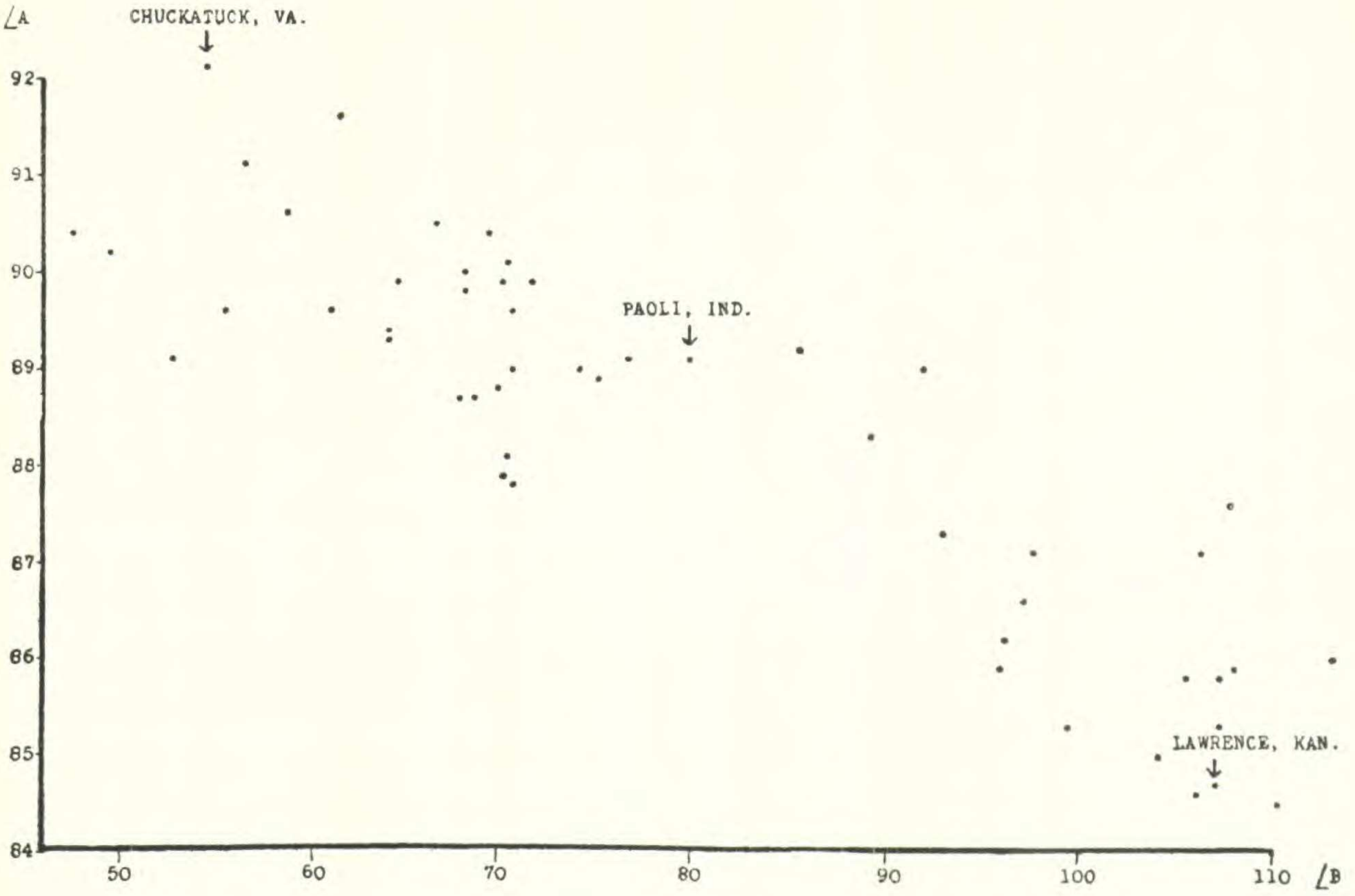


Fig. 5. Coincidence of colonial means for ∠A and ∠B along a roadside profile from eastern Kansas to the coast of Virginia. Explanation in the text.

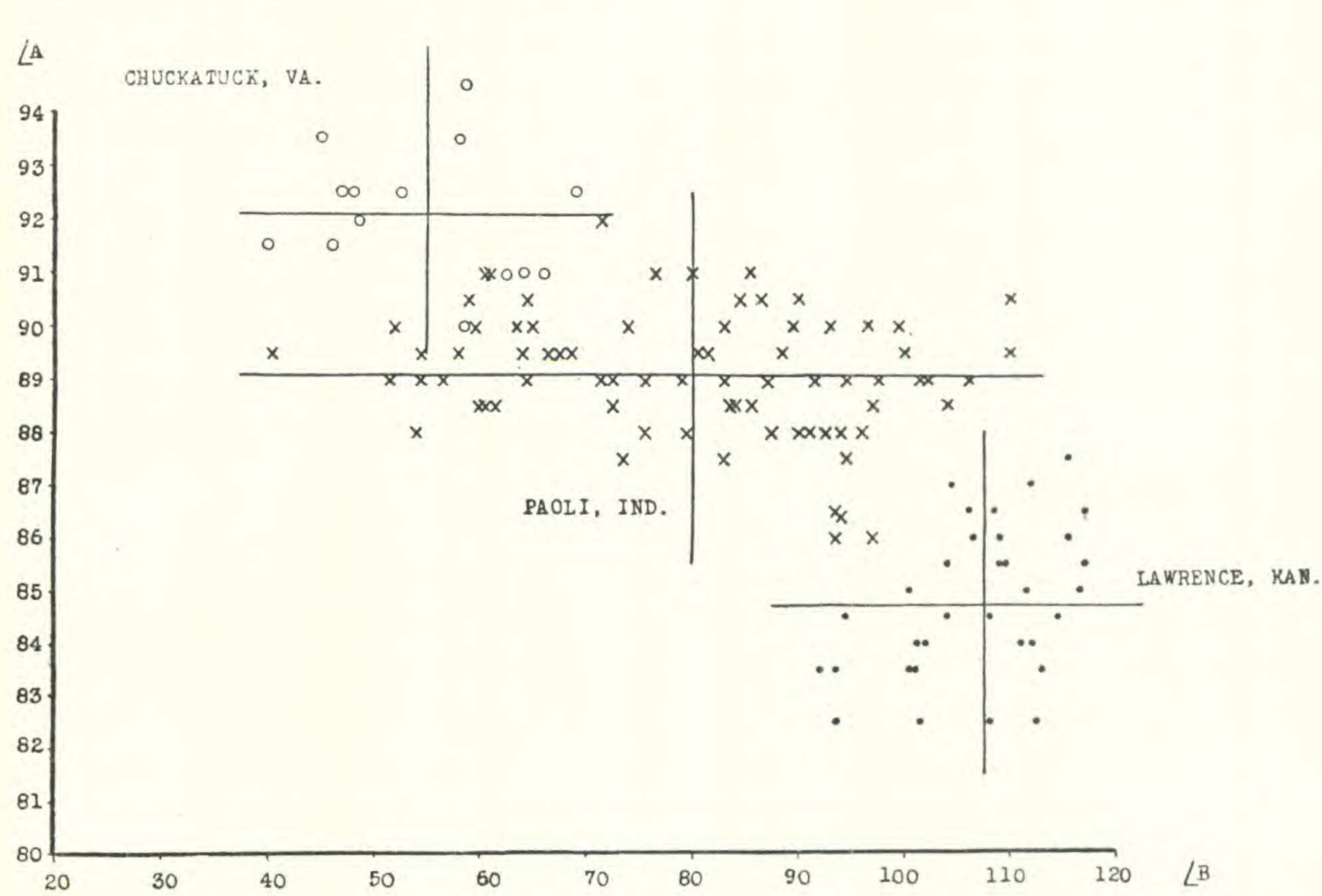


Fig. 6. Relation of ∠A and ∠B values in three colonies of butterflyweed. Explanation in the text.

extending from Topeka, Kansas, to Chuckatuck, Virginia. The close relation of intergrading phenotypes to geographical distribution appears striking, particularly with reference to the intergradation of high ∠A and low ∠B values at the eastern end, and low ∠A and high ∠B values in the west. The three colonies specially identified were chosen not only because they occur at both ends and middle of the distribution, but because their combined means represent satisfactorily the typical parameters of both subspecies and their cline, including sufficient cases for further analysis as well.

In fig. 6, the individual cases for Chuckatuck, Paoli, and Lawrence are superimposed upon the same grid, the three cross-bars indicating the respective coincidences of the means for ∠A and ∠B. The almost perfect confluence of the individual phenotypes of the three colonies, located almost equidistantly along the profile of nearly 1200 miles, is most satisfying.

Quantitative characters, notably leaf shape, usually have been found due to multiple factors exhibiting Mendelian segregation. That such is the case with respect to both ∠A and ∠B in butterflyweed leaves is suggested most forcibly by fig. 6, in which the Paoli colony assumes the properties of an experimentally produced F_2 between the Chuckatuck and the Lawrence populations. The range of ∠B of the former clearly more than equals the combined ranges of the latter two colonies. With respect to ∠A the situation is not so clear, since, although the range of Paoli is greater than that for either Chuckatuck or Lawrence, it is not equal to the combined ranges of the two latter. This, following Muller (1936), would indicate not the absence of multiple genes, but cancellation of variability in the F_2 by the intra-racial variation of the parent strains.

An additional inference to be gleaned from fig. 6 is the apparent absence at least of strong linkage between the genotypes of ∠A and ∠B for both Chuckatuck and Lawrence. In the Paoli colony, however, there is a slight tendency for the association of high ∠A and low ∠B expression, and *vice versa*. I assume this may indicate that the multiple gene complex governing either character is of a relatively high order, and that the genes may be distributed upon several chromosomes, or at least at several loci.

In view of our interpretations of figs. 5-6, it seems clear to me that the constellation of means presented in fig. 5 most probably is the result of the early hybridization of plants of *A. t. tuberosa* and *A. t. interior* at the initial juncture of their ranges, with successive back-crosses to other heterozygotes and the ancestral types producing the remarkably even clines with which we have become familiar. From the inferences which I have made concerning the complexity and distribution of the genotypes, I would expect a high chiasma frequency and abundant crossing-over to catalyze the process which we have been discussing. Equilibrium of the genic diffusion may conceivably be upset by such factors as the erection of sterility barriers, as Mather has suggested, but more particularly by

preponderant selection and migration pressure from one or the other of the introgressing populations, an example of which will be provided in a following section of this study.

COMPARISON OF THE HERBARIUM AND ROADSIDE PROFILES

It happens that the roadside profile just discussed falls for virtually its entirety within the horizontal rank of herbarium quadrats from *F3* to *F12* of the phenocontour maps. A comparison of the two sources of data presents some rather interesting topics for conjecture, and is documented graphically in fig. 7. Herbarium data have been borrowed from Table III; in Table V the roadside data from Table IV have been partitioned according to geographical provenience into a complementary series of quadrat populations which are numbered from *3* to *12* and preceded by the initial *Q*. It is essential, in the discussion which follows, for the reader to understand what I consider to be the important properties of these two samplings.

In the first place, I consider the herbarium data to be the most "normal" information available for the population of *Asclepias tuberosa* as it exists throughout its entire range, for reasons concerning the conditions of their collection which I have discussed previously. I believe that my arguments are substantiated sufficiently by the relatively consistent contours of the maps. The data, as far as the element of place is concerned, represent not one special type of habitat, but the sum-total of all types of environments which have been visited by the innumerable participating plant collectors. As far as the element of time is concerned, the properties of the herbarium data are more abstruse. They all have been collected during the blooming seasons of the plants, but during years as long ago as 1820 and as recent as 1946. A little research upon our collections in the herbarium of the Missouri Botanical Garden reveals that the majority of our specimens were prepared between the years 1890 and 1918. The plants, therefore, can only be said to represent, on the whole, the "recent past."

On the other hand, the roadside data are biased in two very important respects: they have been collected only along main-travelled highways, and only during the early summer of the year 1946. The essence of our contrast, therefore, consists of these two particulars: a "normal" collection, with regard to place, versus a roadside sample; and a collection made in the "recent past," versus a collection made during the year 1946. The latter, of course, is unsatisfactorily vague, but it is the best that can be done at the moment, and may be of some use. Should a collection of butterflyweeds be made for comparison twenty-five or fifty years from now along the route of my roadside profile, measured and treated in the same way, I expect that some interesting facts concerning evolutionary topics may be forthcoming.

Considering the small size of the two samplings, only 117 cases for the herbarium profile of over 1200 miles and 994 cases for the roadside, the first impression of fig. 7 may be the relative agreement of the two sets of curves. A second feature,

TABLE V

DATA FROM TABLE IV REASSEMBLED INTO EQUAL-AREA QUADRATS EQUIVALENT TO THOSE OF TABLE III

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

		∠A			∠B			Length			Width		
Quadrat	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
Q3	152	90.4 ± 0.2	2.1	2.3	64.7 ± 1.3	16.3	25.2	69.1 ± 0.9	11.0	15.9	17.1 ± 0.4	5.0	29.2
Q4	120	89.9 ± 0.2	2.0	2.2	68.1 ± 1.4	15.7	21.6	73.0 ± 1.3	14.6	20.0	19.8 ± 0.5	5.7	28.8
Q5	237	89.1 ± 0.1	1.8	2.0	68.1 ± 1.2	17.8	26.0	79.4 ± 0.9	13.9	17.5	18.1 ± 0.3	5.0	27.6
Q6	32	89.2 ± 0.3	1.9	2.1	64.1 ± 3.2	17.7	27.6	98.8 ± 3.0	16.7	16.9	18.3 ± 0.9	5.2	28.4
Q7	87	89.3 ± 0.1	1.3	1.5	66.7 ± 2.1	19.5	29.2	94.6 ± 1.6	15.0	15.9	18.5 ± 0.5	4.8	25.9
Q8	95	88.8 ± 0.2	1.5	1.7	81.9 ± 1.6	15.7	19.2	94.2 ± 1.4	13.3	14.1	17.8 ± 0.4	3.8	21.4
Q9	13	87.8 ± 0.4	1.5	1.7	97.3 ± 4.0	13.8	14.3	79.1 ± 3.8	13.2	16.7	15.0 ± 0.6	2.2	14.7
Q10	104	87.1 ± 0.1	1.3	1.5	98.4 ± 1.2	12.7	12.9	83.6 ± 1.3	12.8	15.3	16.5 ± 0.4	4.2	25.4
Q11	58	86.0 ± 0.2	1.6	1.9	102.1 ± 1.4	10.8	10.6	83.1 ± 1.4	10.5	12.6	16.3 ± 0.6	4.2	25.8
Q12	96	84.9 ± 0.1	1.4	1.6	108.0 ± 0.8	7.5	6.9	70.5 ± 0.8	7.5	10.6	13.8 ± 0.3	3.1	22.5

which I may not have to point out, is that where there are disagreements of considerable degree, the discrepancies are consistent. These two properties are concomitant, and justify the acceptance of the two sources of data in contrasting their two properties of place and time.

∠A

Herbarium and roadside curves for both the means and standard deviations are very similar, but the curve for the roadside means is much smoother than is that for the herbarium. The consistency of the stepped aspect of the herbarium curve, in my opinion, argues against its interpretation as a statistical artifact, and that introgressive diffusion is unquestionably farther advanced along the roadside. Although the interval range of the *s* curves is almost too close for critical comparison, it will be seen that roughly the eastern half of the roadside profile is more variable than the western half. There is no crest of variability in either the roadside or the herbarium profile.

∠B

The ∠B curves for the means and the standard deviations for herbarium and roadside are more contrasting because of the wider interval ranges. It is seen that west of the Allegheny Mountains (quadrats *12* to *7*) the roadside populations have become somewhat more like the eastern subspecies; that of quadrat *8* (southern Indiana) strikingly so. From the Alleghenies to the Atlantic coast, however, the leaves of the roadside populations have shifted to a conspicuously higher ∠B, indicative of a leaf base more nearly approaching that of the western subspecies. The *s* curves are rather similar, but it probably is significant that variability of the roadside populations west of the Alleghenies has decreased, as a rule, whereas that to the east has been maintained or increased. This is consistent with our interpretation of the curves for ∠A.

LENGTH AND WIDTH

In interpreting the roadside and herbarium profiles, it should be remembered that it was found impossible, in dealing with the phenocontour maps, to plot isophenes for length and width. This apparently was due to the greater genetic drift of those characters in microgeographic races, but chiefly to the fact that the subspecies themselves are not differentiated by size factors.

Consequently, neither are our herbarium and roadside curves for length and width as easy of comparison as are those for ∠A and ∠B. In this case, the difficulty is accentuated because the data for the roadside are composed of relatively few specific colonies (or microgeographic races) which are particularly haphazard in the characters under consideration. Nevertheless, it will be seen that heterosis is suggested by the consistently larger leaves roughly from eastern Kentucky to the Atlantic seaboard, having apparently moved eastward together with the crest of variability of ∠B, as we might expect. The variability in length and width, rather oddly, has not increased notably; rather, the roadside curves have smoothed.

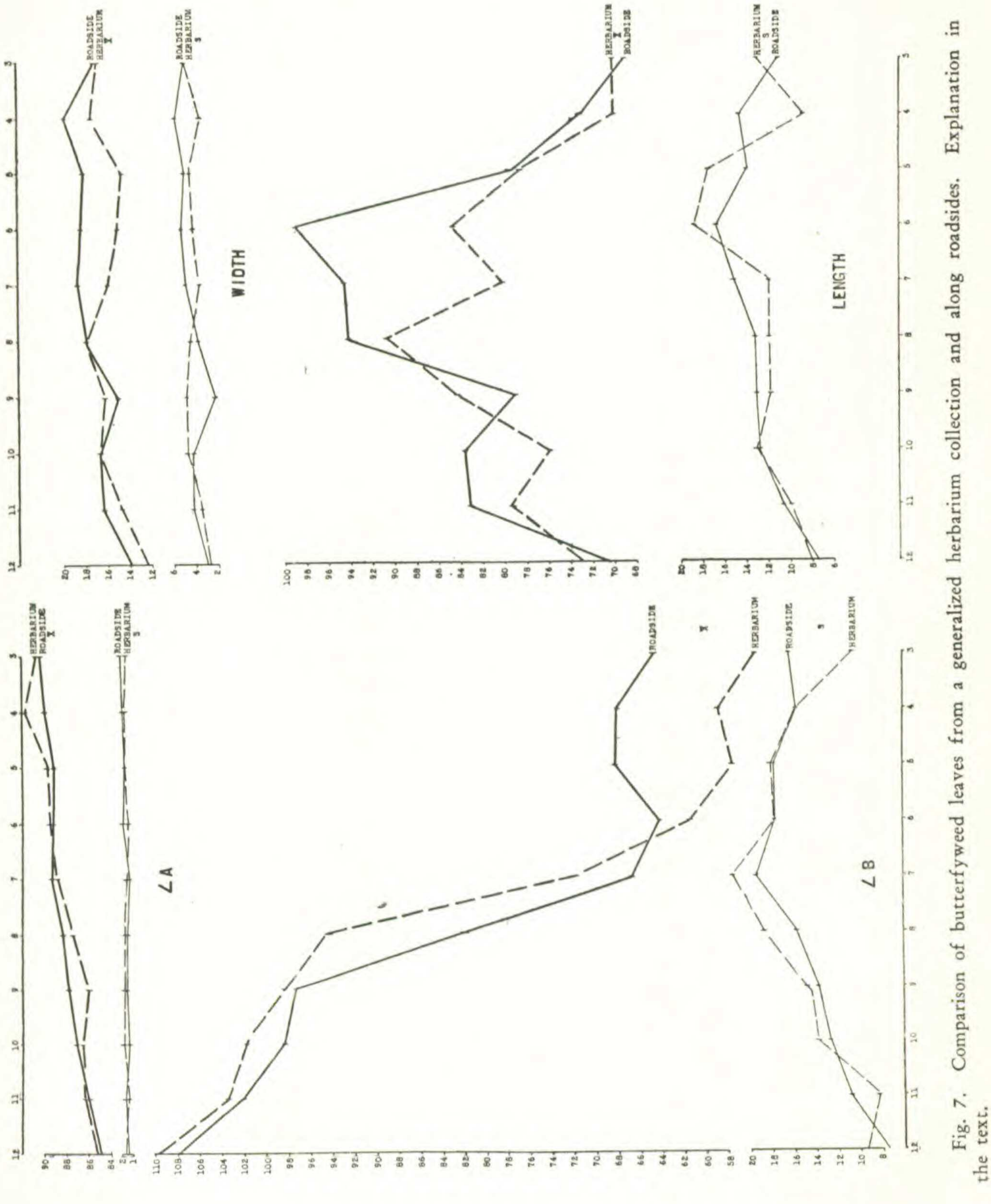


Fig. 7. Comparison of butterfyweed leaves from a generalized herbarium collection and along roadsides. Explanation in the text.

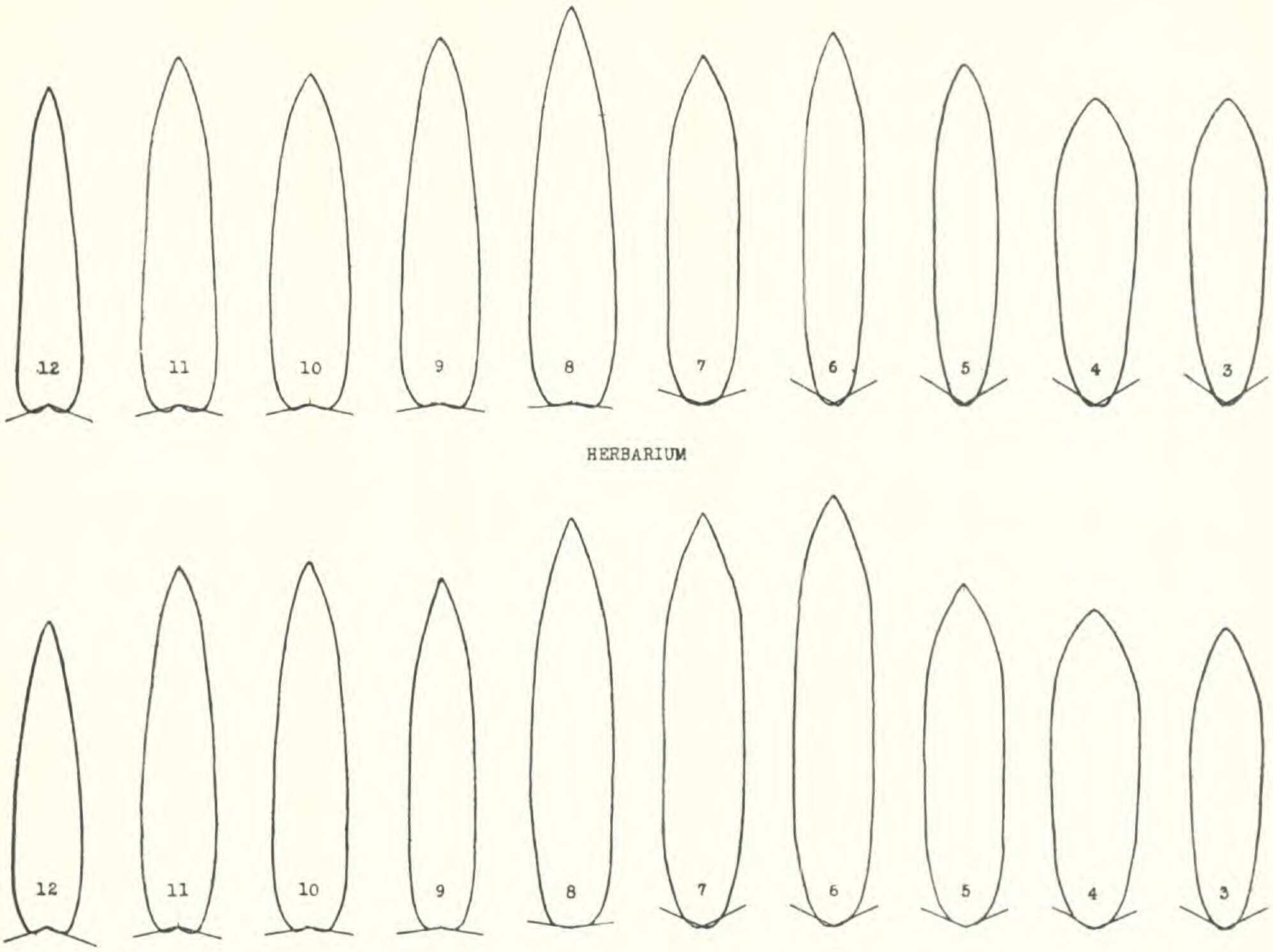


Fig. 8. Reconstruction of butterflyweed leaves from equivalent herbarium and roadside quadrats. Explanation in the text.

I conclude from our examination of the herbarium and roadside profiles that the details of the phenocontour maps obtained from herbarium specimens are reliable under the broad conditions of their compilation. More important, the observations of Wiegand (1935) and others, that hybridization is accelerated along roadsides and in disturbed areas, is affirmed and given quantitative expression.

Figure 8 reproduces models of leaves reconstructed according to the specifications of the ten herbarium and roadside quadrats, to illustrate our discussion pictorially as well as a commentary on our method of measurement. The basal lines by which ∠B is measured are included for the sake of easier comparison.

Figure 9 consists of a series of frequency histograms for ∠A and ∠B along the roadside profile, reassembled according to standard quadrats. The vertical curves connect the means of each histogram, and provide new representations of the clines we have been discussing. The distributions of the ∠A quadrats, considering the size of their samples, are nearly normal throughout. In the histograms for ∠B, however, a consistent positive skewing is noticeable in quadrats *7* to *3*. To the west, in quadrats *8* to *10*, a negative skewness is found, while the distributions of quadrats *11* to *12* are normal or essentially so. In the ∠B, therefore, the

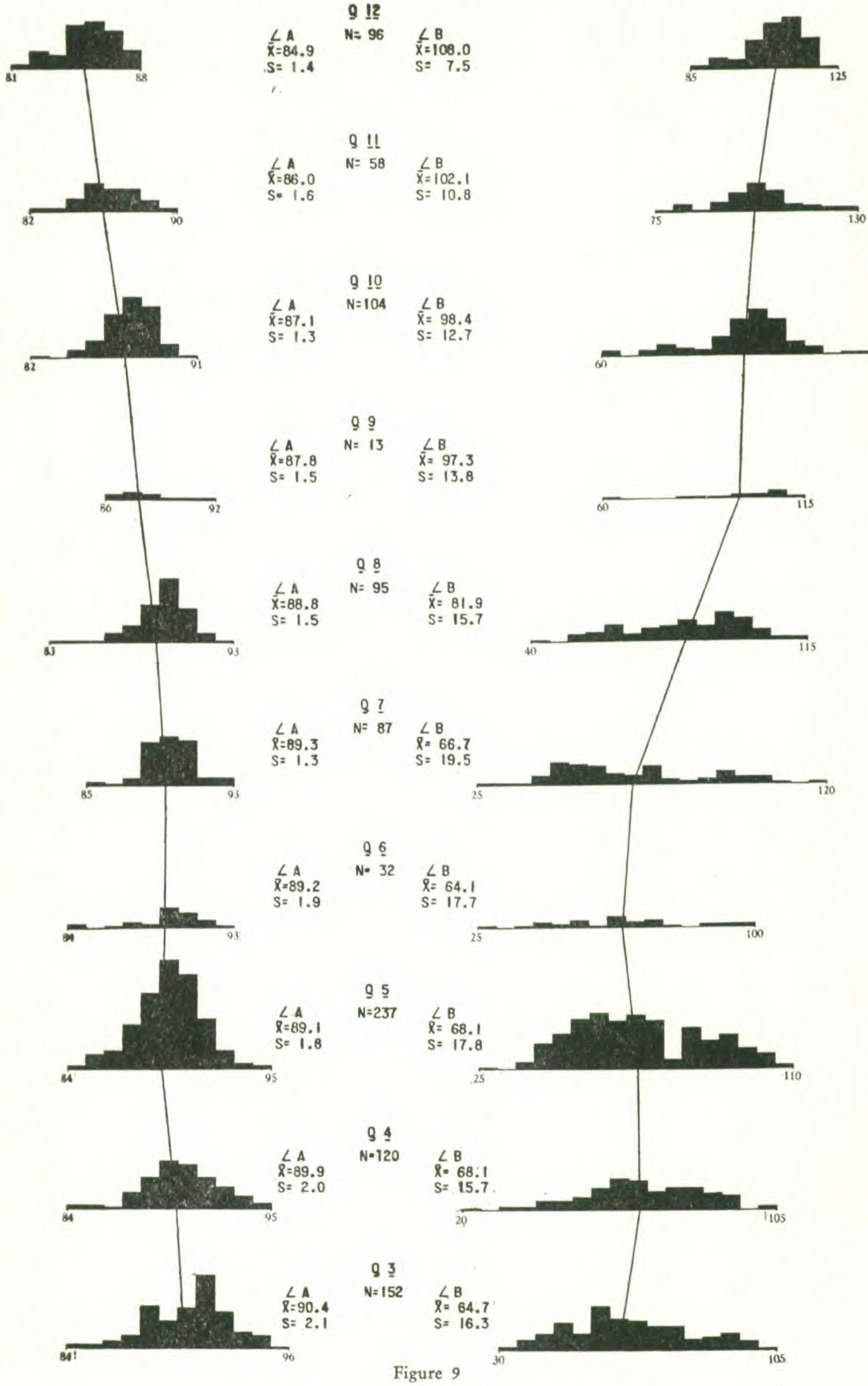

♀ 12
∠ A N= 96 ∠ B
X̄=84.9 X̄=108.0
S= 1.4 S= 7.5
81 88
85 125
♀ 11
∠ A N= 58 ∠ B
X̄=86.0 X̄=102.1
S= 1.6 S= 10.8
82 90
75 130
♀ 10
∠ A N=104 ∠ B
X̄=87.1 X̄= 98.4
S= 1.3 S= 12.7
82 91
60 135
♀ 9
∠ A N= 13 ∠ B
X̄=87.8 X̄= 97.3
S= 1.5 S= 13.8
86 92
60 115
♀ 8
∠ A N= 95 ∠ B
X̄=88.8 X̄= 81.9
S= 1.5 S= 15.7
83 93
40 115
♀ 7
∠ A N= 87 ∠ B
X̄=89.3 X̄= 66.7
S= 1.3 S= 19.5
85 93
25 120
♀ 6
∠ A N= 32 ∠ B
X̄=89.2 X̄= 64.1
S= 1.9 S= 17.7
84 93
25 100
♀ 5
∠ A N=237 ∠ B
X̄=89.1 X̄= 68.1
S= 1.8 S= 17.8
84 95
25 110
♀ 4
∠ A N=120 ∠ B
X̄=89.9 X̄= 68.1
S= 2.0 S= 15.7
84 95
20 105
♀ 3
∠ A N=152 ∠ B
X̄=90.4 X̄= 64.7
S= 2.1 S= 16.3
84 96
30 105

Figure 9

quadrat distributions are skewed in the direction of introgression. The absence of consistent skewness in the ∠A histograms may be ascribed to the relatively less sensitivity of this measure; actually, however, I interpret it to be additional evidence of the quantitative nature of the ∠A genotype in contrast to the qualitative differences of the ∠B genotypes. This question will be considered in detail in a future series of studies on butterflyweed. Another aspect of the skewing of distributions in relation to the direction of gene flow will be presented shortly.

VI. Intra-subspecific Differentiation of *Asclepias tuberosa interior*

In the preceding discussions of the phenocontours of *Asclepias tuberosa,* we found that although minor microgeographic races may be observed in the eastern *A. t. tuberosa,* larger internal patterns, if they exist, are obscured by introgression with neighboring subspecies, the Floridian *A. t. Rolfsii* and the mid-western *A. t. interior.* The last named, however, has a range sufficiently large for us to extract for analysis the vast western portion of its distribution, which is not affected by introgressive gene flow with the eastern subspecies.

In this region, as we have learned from the phenocontours, it is possible to discern certain more or less definite trends in the median length, median width, apical taper (∠A), and nature of the base (∠B) of the leaves. These internal patterns may be rather vaguely distinguished by the method of quadrats through which the phenocontour maps were compiled, but they apparently are of such greater magnitude that they require a different method of analysis. The situation suggests an allegoric parallel with a picture printed by the half-tone process, in which the screened image must be viewed at a certain distance for best comprehension.

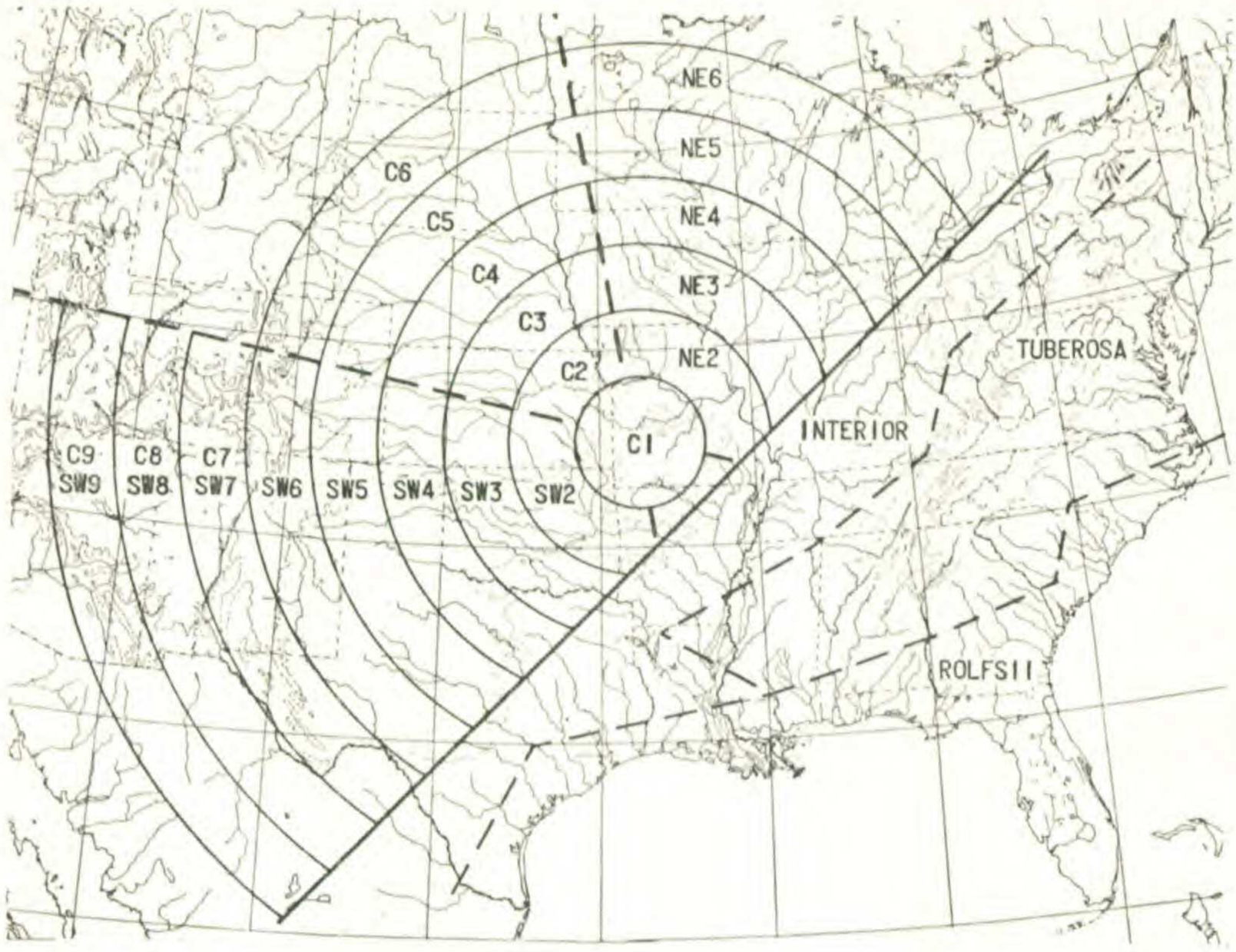
METHODS OF ANALYSIS

Methods for the analysis of the internal differentiation of *A. t. interior* are suggested by the phenocontour maps, in which the primary direction of modification usually is centrifugal from the Ozark plateau, the putative center of origin of the subspecies. This tendency is seen most clearly in the character of the leaf base, designated as ∠B; the leaves in the central Ozarks (*i. e.* quadrats *G11* and *G12*) being deeply cordate as a rule, but becoming successively less cordate in quadrats progressively outward in all directions from this center. At the periphery of the distribution, from southern Canada to northern Mexico, the leaves no longer are cordate, but more or less rounded or cuneate at the base, as in the eastern subspecies.

In Map VII, an arbitrary, solid line is drawn roughly from Toronto, Ontario, through San Antonio, Texas, and produced considerably to the southwest of the latter city; it is approximately midway between the central Ozarks and the crest of variability of the ∠B phenocontour map. To the right of this line, popu-

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Fig. 9. ∠A and ∠B frequency histograms of butterflyweed leaves along a roadside profile, assembled into equivalent profiles. Explanation in the text.



Map VII. Method of study of intra-subspecific differentiation in *Asclepias tuberosa interior* by means of equidistant concentric circles.

lations of *A. t. interior* are increasingly affected by introgression with the eastern subspecies; to the left, evidence of introgression is absent or negligible. Any internal modification of ∠B which we will find in "true" ssp. *interior* surely must be taken into account in its effect on introgression with ssp. *tuberosa*, but we shall defer that aspect of the problem for the moment, confining our attention to strictly intra-subspecific differentiation to the left of our arbitrary boundary.

Since modification within *A. t. interior* is believed to be centrifugal from the central Ozarks, it is legitimate to test the hypothesis by projecting upon a map a series of equidistant concentric circles emanating from that point; this is accomplished in Map VII by using a center exactly midway between quadrats *G11* and *G12*. Our procedure obviously must be made to agree as far as possible with the system of 120-mile quadrats previously employed in the phenocontour maps; consequently, the first circle, labelled *C1*, is inscribed with a radius of 120 miles about quadrats *G11* and *G12*. The compass is then widened to increase the radius by 120 miles and a second circle is drawn outside *C1* and enclosing the circular area labelled as *C2*. In the map, this circle actually is drawn only to the left of the arbitrary solid line, but its course to the right must be visualized for the benefit of discussion which will follow. For our immediate purpose, *C2* is an arc rather than a circle. In the other circles, to *C6*, the same procedure is followed. Because *A. t. interior* extends farther to the southwest than to the northeast, the

outermost "circles" are lesser arcs touching the arbitrary solid line at only one point, but they, too, may be visualized as extending to the southeast of the introgression boundary, and thus are designated as *C7*, *C8*, and *C9*.

In reassigning statistics from the quadrats of the previous maps to the new circular populations, the arbitrary procedure is adopted of transfering to a given circle the data of only those quadrats whose exact center lies within its boundaries. Thus, in *C1*, although the periphery of the area intersects four other quadrats, only the centers of quadrats *G11* and *G12* satisfy our conditions, and the data of the other four are assigned, together with others similarly chosen, to *C2*. Similar assignment is practiced in the remaining circles.

An additional feature of Map VII which requires explanation are the two broken lines which intersect in the center of *C1*. These lines are drawn in order to separate from the concentric circles two equivalent series of concentric arcs lying in opposed directions, one to the northeast and labelled from *NE2* to *NE6*, the other to the southwest and labelled from *SW2* to *SW9;* the purpose of these will be explained shortly. Rather confusingly, I am afraid, the three southwesternmost arcs bear two sets of symbols, *C7* to *C9* and *SW7* to *SW9* for designation in different phases of our discussion, but the populations are the same.

THE EVIDENCE OF INTERNAL DIFFERENTIATION

∠B

Since our circle and arc populations will be provided by the quadrats of the phenocontour maps, two ways of using the quadrats in their new groupings suggest themselves, which we will illustrate with regard to the data for ∠B. In Table VI, the herbarium quadrats assigned to each circle have been broken down and the constituent cases thrown together in computing new circle means and the usual measures of variance. The centrifugal lowering of ∠B values which was intimated in an irregular fashion by the phenocontour map is seen to be a consistent tendency. In Table VII, on the other hand, the means of the means and the means of the standard deviations of the included quadrats of each circle are computed for comparison. Only slight deviations from the statistics of Table VI are found, and the centrifugal tendency is confirmed by either procedure.

It will be appreciated, however, that a curve drawn to the data of Table VII would be somewhat smoother than one drawn to the data of Table VI. I assume this to be due to unequal weighting caused by the numerous cases in well-collected quadrats and the fewer cases in quadrats less frequented by plant collectors. This inequality appears to be compensated in the calculation of the means of means and means of standard deviations, since a quadrat containing few cases is weighted equally to a quadrat containing many cases. In addition, of course, the method of Table VII is more convenient than that of Table VI; consequently I have used the former in subsequent computations.

The data of Table VII are presented graphically in fig. 10, in which the ordinate is in degrees of ∠B and the abscissa represents the equidistant circles

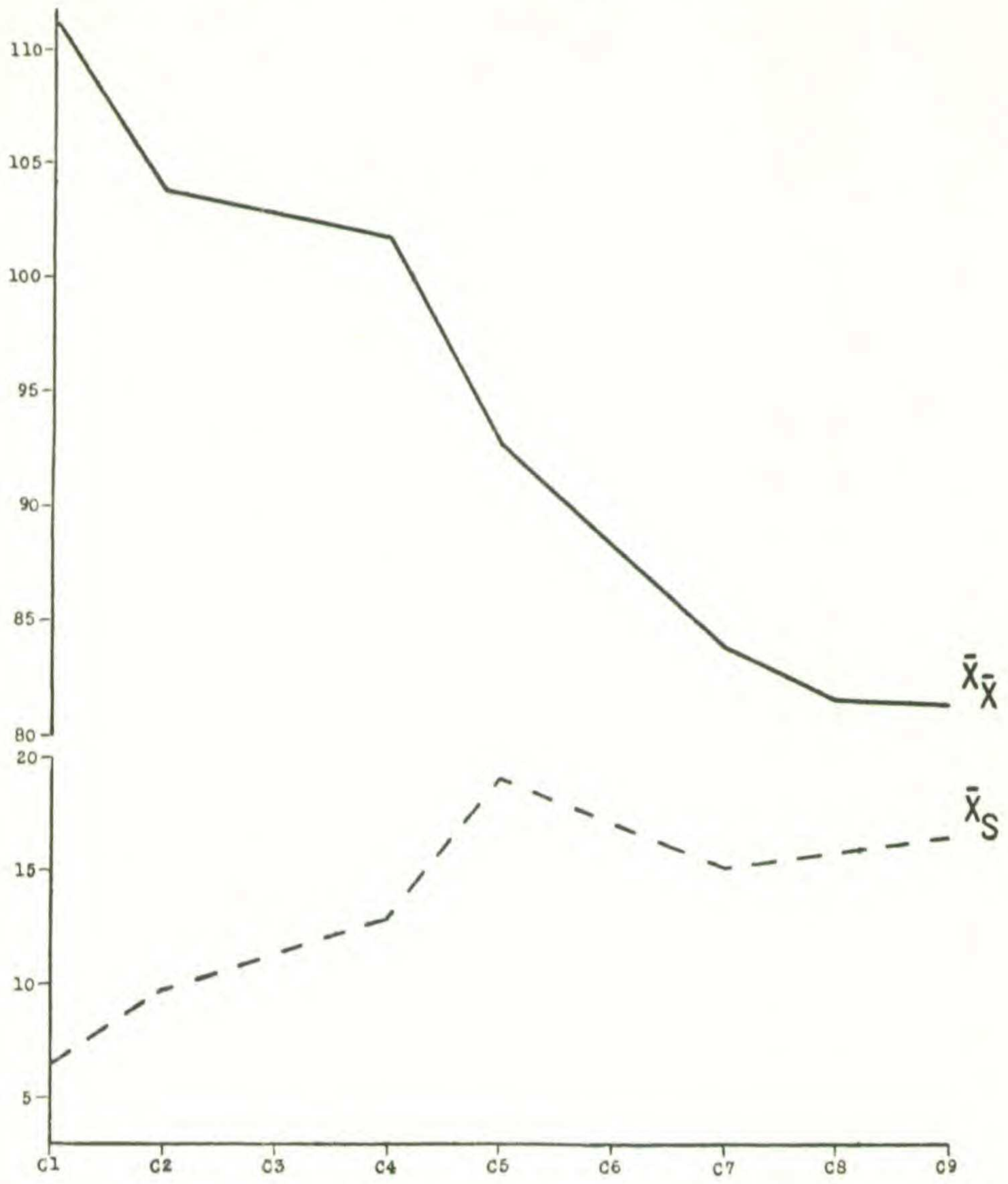


Fig. 10. ∠B means of means and means of standard deviations of *Asclepias tuberosa interior* in the central Ozarks and in equidistant concentric circles to the periphery of the subspecies range. Explanation in the text.

from the Ozark plateau. The means curve is seen to be remarkably even, with the exception of the interesting "hump" at circles *3* to *4*. The curve for the standard deviation means is still more interesting, since it rises from the lowest value, in circle *1* to a crest at circle *5;* then subsides to a somewhat lower plateau for the outermost circles.

The validity of the curves presented in fig. 10 may be tested by dividing the concentric circles into two equal, but opposed, series of concentric arcs to the southwest and to the northeast of the Ozark plateau. The primary purpose of these arcs is to withdraw for comparison two equivalent samples from the original populations; to further this end, the opposed arcs are isolated by the series of arcs to the northwest, upon which the labels of the circles appear. An additional advantage of our two series of arcs is that they traverse climatic regions which differ to a very marked degree: from the deserts of the southwestern United States and northern Mexico to the Ozarks, and from the Ozarks to the continental forests of

TABLE VI

∠B INDIVIDUAL CASES OF HERBARIUM QUADRATS REASSEMBLED INTO CONCENTRIC CIRCLES

(Means, standard errors, standard deviations, and coefficients of variation)

Arc	C1	C2	C3	C4	C5	C6	C7	C8	C9
N	31	213	223	176	225	85	44	32	64
$\bar{X}$	111.1 ± 1.2	104.2 ± 0.7	103.4 ± 0.8	100.1 ± 1.1	97.8 ± 1.2	84.5 ± 2.1	81.2 ± 2.5	83.6 ± 3.1	80.2 ± 2.1
s	6.4	10.0	12.0	14.8	18.0	18.9	16.5	17.4	16.6
V	5.8	9.6	11.6	14.8	18.4	22.4	20.3	20.8	20.7

TABLE VII

∠B MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	C1	C2	C3	C4	C5	C6	C7	C8	C9
N	2	9	10	8	13	8	8	4	7
$\bar{X}_{\bar{x}}$	111.2	103.8	102.7	101.8	92.8	88.4	83.9	81.6	81.4
$\bar{X}_s$	6.5	10.2	11.6	12.8	19.1	17.2	15.2	15.9	16.5

the Great Lakes. Thus we may expect to observe any influence of climate upon the phenotypic gradient.

Two final properties of the arc populations are worthy of attention. The northeastern arcs lie almost wholly in territory covered by the last glaciation, whereas the southwestern arcs apparently have been available for plant occupancy since the beginning of the Mesozoic or before. Furthermore, we have observed that colonies of butterflyweed are appreciably larger and more frequent in the northeastern arc, whereas in the southwestern arc the colonies are both smaller and more isolated. We may expect the three factors of climate, geological history, and relative population structure to have characteristic effects upon the internal differentiation of butterflyweed, as in other organisms. The method of analysis by two opposed arcs has so many advantages that it has been used not only with regard to ∠B, but to ∠A, median length, and median width as well. For the moment, however, we shall confine our attention to the first named.

Data for ∠B, analyzed by means of the two opposed arcs, are provided in Table VIII. In the uppermost panel of fig. 11, the data are presented graphically in a manner designed to simulate the geographic relationship of *CI* and the two sets of arcs, the ordinate scales in degrees being erected at the center, and the two sets of curves diverging to left (southwest) and right (northeast) respectively. The two sets of curves are strikingly similar, and both obviously confirm those previously obtained from the circle populations. Climate is seen to have nothing to do with expression of the phenotype.

The chief disagreement between the circle and the arc data is seen to be the accentuation of the "hump" of the means curves previously noted, occasioned by the relatively low values of arcs *2* and *3* in both the southwestern and the northeastern series. I assume this effect to be due to the failure of the diagonal, solid line noted in connection with Map VII entirely to exclude the influence of introgression with the eastern subspecies, and that the actual curves, if introgression were quite eliminated, would be appreciably smoother even than as depicted in fig. 10. I have not attempted to move the diagonal line farther to the left, however, because such action would result in reducing our populations sufficiently to impede our calculations. We are justified, however, in regarding the smooth means gradient of fig. 10 as being an understatement rather than an exaggeration.

It is important, finally, to emphasize the confirmation by the opposed arcs not only of the means of means presented in fig. 10, but also of the peculiar curve for the means of standard deviations, with its interesting crest of variability at circle *5*. It is important, also, to call attention to the similarity of this curve to the gradient of the standard deviations involved in the introgression of subspecies *interior* and *tuberosa* which were presented in fig. *7*.

The basic similarity of the gradients representing the introgression of subspecies *interior* and *tuberosa* (fig. *7*) and those involved in the internal differentiation of ∠B in *interior* strongly suggests that somewhat similar processes are in play. This is indicated most particularly by the confirmation of the crest of variability midway in the arc and circle gradients.

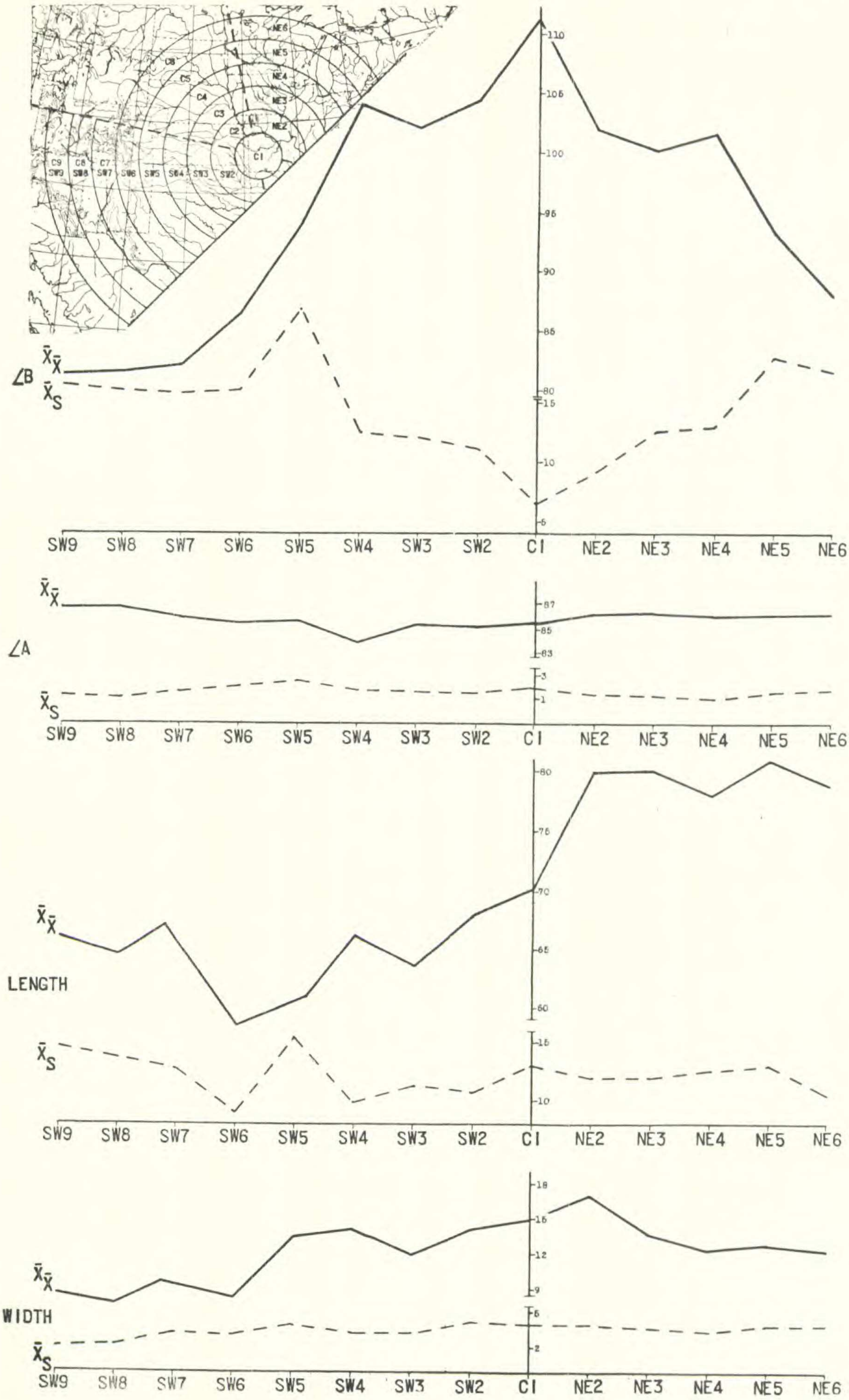


Fig. 11. Means of means and means of standard deviations of ∠B, ∠A, median length, and median width of *Asclepias tuberosa interior* in the central Ozarks and in equidistant series of arcs to the southwest and northeast. Explanation in the text.

TABLE VIII

∠B MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES
(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	3	4	4	2	3	3	4	7	4
$\bar{X}_{\bar{x}}$	81.4	81.6	82.1	85.4	94.1	104.0	102.1	104.4	111.2	101.9	100.2	101.6	93.4	87.9
$\bar{X}_s$	16.5	16.1	15.8	16.0	22.9	12.5	12.1	11.2	6.5	9.2	12.6	13.0	18.7	17.6

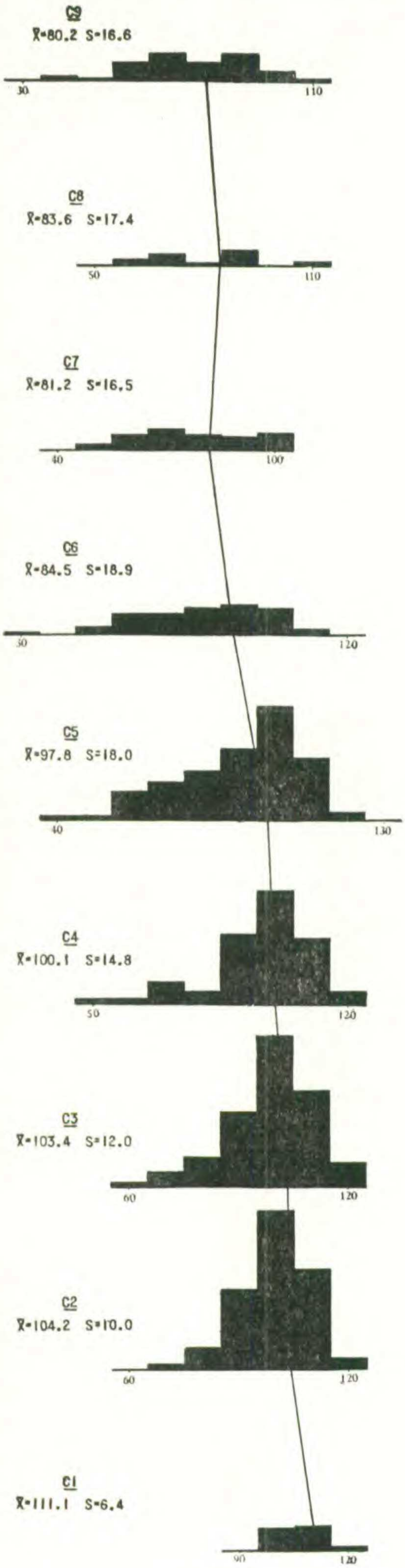
Since the gradients of the opposed arcs in glaciated and in unglaciated territory are essentially similar, I believe that we may visualize the leaves of *A. t. interior* in post-Pleistocene times, throughout its range, as being essentially like those with rounded to cuneate bases predominant to-day at the periphery of its distribution. In relatively recent times, probably only a few thousand years ago, a major genotypic change producing a deeply cordate leaf base would appear to have become established in the central Ozarks, and subsequently to have been diffused to outlying populations in the centrifugal manner which we have been discussing.

In the absence of detailed breeding and cytological evidence, we may only conjecture concerning the nature of this genic change. It is apparently multifactorial, as evidenced by the properties of its distributional frequencies (cf. fig. 12). One would expect a single mutation, even if having sufficient survival value, to be inoperative, and the simultaneous production of a sufficiently large number of concomitant mutations effecting the same character to be extremely unlikely. Since either translocation or inversion would be expected to reduce the frequency of crossing-over, it is difficult to see how the smooth gradient involved in the centrifugal modification of ∠B could be obtained through chromosomal rearrangement, as understood at present. I have in progress further genetical studies, which I hope will throw some light upon the nature of the supposed genotypic renovation of *A. t. interior*.

In this connection, however, it is worthy of note that I have found plants of the cordate-leaved populations of *A. t. interior* consistently to have more stems per plant, as well as more leaf nodes per stem, than in plants of the peripheral, narrow-based populations. It is natural to ascribe selective advantage to the former, because of their presumably greater reproductive potential, and we shall encounter confirmative statistical evidence of this inference presently.

Figure 12 consists of standard frequency histograms of ∠B in the nine circles extending from the central Ozarks to the periphery of the range of *A. t. interior* (exclusive of the zone of introgression with *A. t. tuberosa*). The vertical curve connects the means of the several histograms. Although surely distorted by the discrepant sample sizes, the symmetry of the distributions is remarkable in passing, centrifugally, from essential normality through increasing degrees of negative skewness to a less skewed, platykurtic form near the center of the gradient; the remaining figures become increasingly bimodal. An intimation of this trend was seen previously in the histograms of the roadside profile (fig. 9), in which the figure for *Q11* (partly within *C1*) is normal, whereas that for *Q12* (wholly within *C2*) is negatively skewed.

In connection with fig. 9, we remarked that skewing of the distributions is rather consistently in the direction of the introgressing subspecies parameters, and thus that it points toward the direction of gene flow. A more likely explanation of the skewing, however, is provided in fig. 12, which happens to be *away* from the direction of gene flow. In other words, skewing in these figures does not indicate the direction of gene flow, but probably merely the distribution of domi-



nance, as suggested by Fisher, Immer, and Tedin (1932). Consequently, in the gradual development of bimodality toward the periphery of the range, we might infer the gradual loss of dominance in both types. I assume that if our range were sufficiently great, we might thereafter witness the emergence of increasing dominance of the ancestral genotype.

Although it may be rather rash to continue speculation, I am inclined toward the opinion that in the centrifugal differentiation of ∠B within *A. t. interior*, as in the introgression of that subspecies with *A. t. tuberosa*, genic amalgamation is effected by migration, cross-fertilization, and redistribution of the genotypes through crossing-over. I would assume the bimodality of our peripheral populations to indicate relatively early steps in this process. The eventual emergence of the Ozark strain as dominant I would predict by virtue of its supposed selective advantages.

At this point I would wish to insert an analysis of a roadside profile from the central Ozarks through the circles, similar to that by which the introgression of subspecies *interior* and *tuberosa* was studied. Since circumstances have prevented me from gathering the necessary data, Table IX is substituted, in which will be found statistics of a random assortment of natural butterflyweed colonies collected in the central Ozarks and in the southwestern and northeastern arcs. As incomplete as the evidence may be, we may observe additional confirmation of the centrifugal effect; we may see that here, also, as in the introgressing subspecies, redistribution of the genotypes is not an orderly diffusion, but proceeds from colony to colony with different

Fig. 12. Distribution of ∠B in 9 equidistant circles from the central Ozarks to the periphery of the range of *A. t. interior*. Explanation in the text.

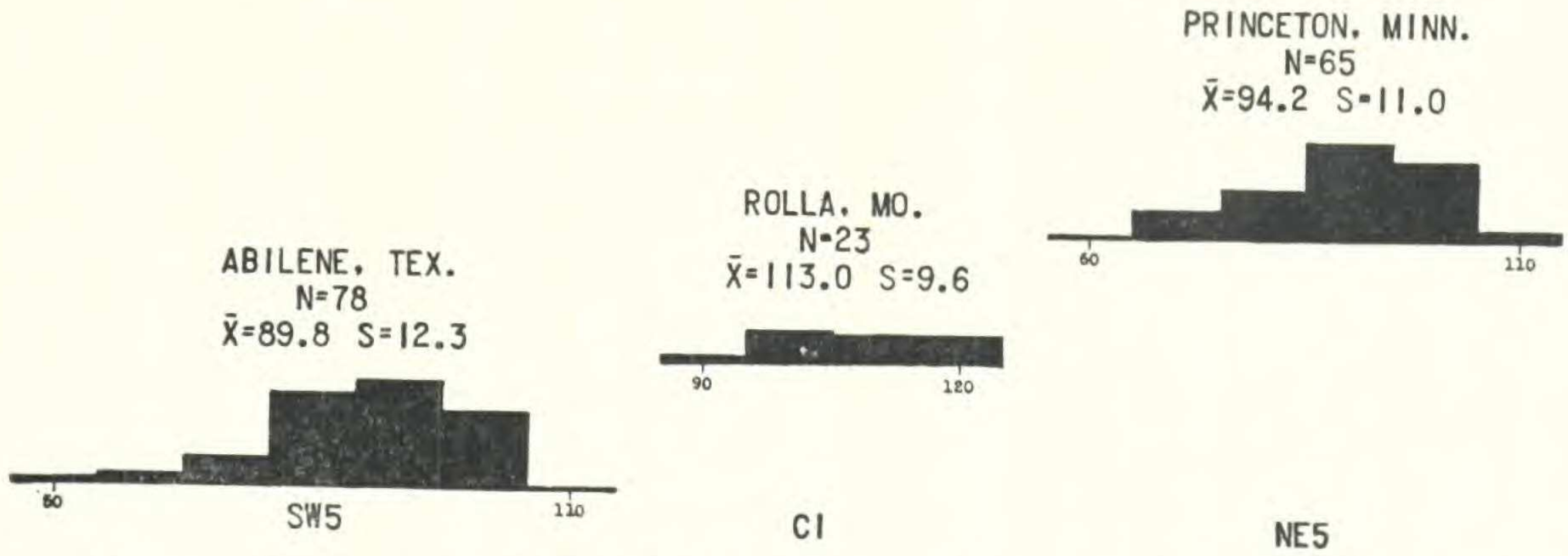


Fig. 13. Distribution of ∠B in 3 colonies of *A. t. interior*. Explanation in the text.

velocity rates, depending on the genic constitution of the reproducing zygotes.

Figure 13 consists of frequency histograms of three natural colonies of *A. t. interior:* one drawn from the central Ozarks, the other two from arcs *SW5* and *NE5*, from left to right, respectively. The figures confirm the properties of the artificial populations which were discussed with reference to fig. 12. Bimodal distributions from the far southwest are not available because of the small population sizes in that region.

If we return, in closing, to the complementary curves for ∠B in the southwest and northeast arcs, reproduced in the uppermost panel of fig. 11, we may remember that the first evidence of the genetic basis of the centrifugal effect was received in view of the very great climatic difference of the territories included. Whether toward the Sonoran deserts or the Canadian forests, the phenotypic gradients apparently are not directly affected. That is to say that the concentric lowering of ∠B values, *per se*, is not environmental.

In the relative rates of transmission of the new gene arrangement, however, there is evidence that climate plays a positive role. For in the more equable climates of the northeastern arcs, the gradient for the means of means is more smooth than is that in the hotter, more arid southwestern arcs, and the means of the corresponding arcs are consistently somewhat lower. The curve for the means of standard deviations is more even in the northeastern arcs as well, and the crest of variability is somewhat lower. Genic diffusion obviously is more rapid in the northeastern arcs because the favorable climate allows the incidence of both larger and more frequent colonies of the plant.

In the remaining paragraphs of this section, the data for ∠A, median length, and median width are treated similarly by the comparison of the southwestern and northeastern arc populations. Data are provided in Tables X, XI, and XII, respectively, and presented graphically in fig. 11. In all three characters evidence of genetic drift, with or without the directing influence of natural selection, appears to be the chief phenomenon of interest.

Before continuing, it may be well to emphasize again what I take to be the most important properties of the two series of arcs in this connection, *viz.*, the rather uniformly equable climate of the northeastern arcs, with their relatively

TABLE IX

MEASUREMENTS OF LEAVES OF *ASCLEPIAS TUBEROSA INTERIOR* ASSEMBLED ACCORDING TO NATURAL COLONIES FROM NORTHEAST TO SOUTHWEST OF THE SUBSPECIES RANGE

(Means, standard errors, standard deviations, and coefficients of variation; angles in degrees, length and width in millimeters)

Arc	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
NE5	Long Siding, Mille Lacs Co., Minn.	8	86.9 ± 0.5	1.3	1.5	82.6 ± 4.7	12.4	15.0	82.9 ± 5.0	13.1	15.8	12.5 ± 1.4	3.6	28.8
"	Princeton #1, Sherburne Co., Minn.	65	86.1 ± 0.2	1.4	1.6	94.2 ± 1.4	11.0	11.7	83.8 ± 1.4	11.3	13.5	12.9 ± 0.4	3.1	24.0
"	Princeton #2, Sherburne Co., Minn.	29	87.9 ± 0.1	0.6	0.7	90.9 ± 2.0	10.8	11.9	79.4 ± 2.0	10.4	13.1	9.8 ± 0.3	1.7	17.3
"	Elk River #1, Sherburne Co., Minn.	31	87.2 ± 0.2	1.3	1.5	91.5 ± 1.8	10.1	11.0	82.5 ± 2.1	11.4	13.8	12.0 ± 0.4	2.2	18.3
"	Elk River #2, Sherburne Co., Minn.	22	85.9 ± 0.4	1.8	2.1	88.6 ± 3.2	14.7	16.6	83.5 ± 2.4	11.0	13.2	13.3 ± 1.1	5.1	38.3
"	Elk River #3, Sherburne Co., Minn.	23	86.5 ± 0.2	0.9	1.0	89.6 ± 2.9	13.5	15.1	86.3 ± 2.4	11.4	13.2	11.3 ± 0.4	1.7	15.0
"	Snail Lake #1, Ramsey Co., Minn.	31	87.2 ± 0.2	1.2	1.4	85.4 ± 3.0	17.4	20.4	77.7 ± 2.8	15.6	20.1	10.2 ± 0.6	3.0	29.4
"	Snail Lake #2, Ramsey Co., Minn.	28	86.2 ± 0.2	1.2	1.4	85.4 ± 2.3	12.1	14.2	80.8 ± 1.8	9.4	11.6	11.5 ± 0.5	2.5	21.7
"	Snail Lake #3, Ramsey Co., Minn.	55	87.8 ± 0.2	1.2	1.4	86.7 ± 2.1	15.3	17.6	84.2 ± 1.6	11.7	13.9	10.5 ± 0.3	2.4	22.8
"	Cannon Falls #1, Dakota Co., Minn.	17	85.6 ± 0.3	1.3	1.5	95.2 ± 1.8	7.3	7.7	86.5 ± 2.8	11.0	12.7	12.9 ± 0.6	2.4	18.6
"	Cannon Falls #2, Dakota Co., Minn.	7	87.6 ± 0.3	0.7	0.8	101.4 ± 3.4	9.1	9.0	85.0 ± 3.6	9.4	11.1	10.4 ± 1.0	2.7	25.9
"	Hampton, Dakota Co., Minn.	4	87.8 ± 0.4	0.9	1.0	79.1 ± 2.6	5.2	6.6	86.0 ± 2.6	11.2	13.0	11.0 ± 1.1	2.2	20.0
"	River Falls, Pierce Co., Wis.	11	85.6 ± 0.3	0.9	1.2	91.4 ± 2.7	8.4	9.2	89.5 ± 3.0	9.5	10.6	15.1 ± 0.3	1.0	6.6
"	Hertel, Burnet Co., Wis.	11	84.8 ± 0.6	1.8	2.1	91.5 ± 2.3	7.5	8.2	83.7 ± 2.7	8.4	10.0	11.8 ± 0.5	1.7	14.3
"	Kalamazoo, Schoolcraft Co., Mich.	13	86.5 ± 0.3	1.0	1.2	107.1 ± 1.7	6.1	5.7	93.5 ± 3.1	11.0	11.8	19.5 ± 0.8	2.8	14.4
NE4	Silver Lake, Palo Alto Co., Iowa	20	85.5 ± 0.2	0.8	0.7	112.8 ± 1.5	6.8	6.0	86.4 ± 1.6	7.0	8.1	13.0 ± 0.3	1.1	8.5

TABLE IX *(Continued)*

Arc	Colonies		∠A			∠B			Length			Width		
	Location	N	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V	$\bar{X}$	s	V
NE4	Ruthven, Clay Co., Iowa	8	85.9 ± 0.2	0.4	0.5	110.9 ± 1.9	4.9	4.4	71.2 ± 2.8	7.2	10.1	10.0 ± 0.8	2.1	21.0
NE3	Wilton Junction, Muscatine Co., Iowa	12	86.5 ± 0.3	0.9	1.0	103.8 ± 3.0	9.8	9.4	99.2 ± 3.9	13.0	13.1	17.5 ± 1.2	3.8	21.1
”	Pocahontas, Pocahontas Co., Iowa	23	86.0 ± 0.4	1.9	2.2	103.9 ± 2.8	12.6	12.1	68.9 ± 2.1	10.0	14.5	10.0 ± 0.5	2.5	25.0
NE2	Murray, Clarke Co., Iowa	25	86.3 ± 0.3	1.5	1.7	103.5 ± 0.5	2.8	2.7	74.1 ± 2.3	11.1	15.0	10.5 ± 0.6	3.1	29.5
”	La Plata, Macon Co., Mo.	19	86.4 ± 0.4	1.5	1.7	98.3 ± 2.3	9.6	9.8	80.4 ± 2.3	11.2	13.9	14.0 ± 0.9	3.7	26.4
C1	Stanton, Franklin Co., Mo.	20	84.6 ± 0.6	2.6	3.1	99.3 ± 2.8	12.4	12.5	87.6 ± 3.4	15.0	17.2	18.8 ± 1.1	4.9	27.1
”	Rolla, Phelps Co., Mo.	23	86.5 ± 0.2	1.2	1.4	113.0 ± 2.0	9.6	8.5	76.7 ± 2.8	13.1	17.1	16.8 ± 0.9	4.4	20.2
SW3	Claremore, Rogers Co., Okla.	8	84.4 ± 0.4	1.0	1.2	115.1 ± 1.2	3.2	2.8	72.0 ± 5.7	14.8	20.6	12.1 ± 1.5	3.8	31.4
”	Hugo, Choctaw Co., Okla.	28	86.1 ± 0.3	1.4	1.6	111.2 ± 1.5	7.8	7.0	79.8 ± 2.1	11.0	13.8	13.7 ± 0.7	3.6	26.3
”	Colgate, Coal Co., Okla.	7	84.7 ± 0.3	0.8	0.9	99.5 ± 2.2	5.5	5.5	46.0 ± 3.2	7.9	17.2	9.9 ± 0.8	1.9	19.2
SW5	Hays, Ellis Co., Kans.	14	83.9 ± 0.4	1.5	1.8	111.7 ± 1.7	6.1	5.5	73.2 ± 2.9	10.4	14.2	17.2 ± 1.1	3.9	22.7
SW6	Abilene, Callahan Co., Tex.	78	84.7 ± 0.2	2.0	2.4	89.8 ± 1.4	12.3	13.7	55.9 ± 0.4	3.7	6.6	10.9 ± 1.1	9.6	17.2
SW7	Guadalupe Mts., Eddy Co., N. M.	6	85.8 ± 0.5	0.8	0.9	90.3 ± 2.9	5.0	5.5	92.3 ± 4.2	7.2	7.8	11.5 ± 0.6	1.0	8.7
SW8	McKittrick Canyon, Culberson Co., Tex.	6	86.9 ± 0.4	0.8	0.9	90.7 ± 5.7	12.8	14.1	79.7 ± 7.9	17.6	22.1	10.9 ± 1.1	2.6	23.8
	Pinos Altos Mts., Grant Co., N. M.	3	86.0 ± 0.6	0.9	1.0	72.0 ± 6.9	9.7	13.5	55.3 ± 4.5	6.4	11.6	7.0 ± 0.7	1.0	14.3

TABLE X

∠A MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	5	4	4	2	3	3	4	7	4
$\bar{X}_{\bar{x}}$	87.7	86.7	85.9	86.4	85.6	83.8	85.4	85.2	85.5	86.2	86.4	86.1	86.2	86.3
$\bar{X}_s$	1.3	1.1	1.6	2.1	2.6	1.8	1.7	1.6	2.0	1.5	1.4	1.1	1.7	1.9

TABLE XI

MEDIAN LENGTH MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	5	4	4	2	3	5	4	7	4
$\bar{X}_{\bar{x}}$	66.0	64.5	67.0	58.3	60.8	66.1	63.5	67.9	70.1	80.0	80.1	78.0	80.9	78.8
$\bar{X}_s$	14.6	13.7	12.7	8.9	15.4	9.8	11.3	10.7	13.0	12.0	12.0	12.6	13.0	10.5

TABLE XII

MEDIAN WIDTH MEANS OF HERBARIUM QUADRATS REASSEMBLED INTO OPPOSED ARCS OF CONCENTRIC CIRCLES

(Means of means and means of standard deviations)

Arc	SW9	SW8	SW7	SW6	SW5	SW4	SW3	SW2	C1	NE2	NE3	NE4	NE5	NE6
N	7	4	6	2	4	5	4	4	2	3	5	4	7	4
$\bar{X}_{\bar{x}}$	8.5	7.7	9.6	8.3	13.5	14.1	12.0	14.1	15.0	17.0	13.7	12.4	12.8	12.4
$\bar{X}_s$	2.0	2.2	3.2	3.1	3.9	3.3	3.3	4.2	4.0	4.0	3.8	3.4	3.9	4.0

larger and more frequent colonies of butterfly-weed; and the increasingly hot, arid climate of the southwestern arcs, in which the colonies are observed to become smaller and less frequent. Of less obvious bearing to our discussion is the probability that the southwestern populations are of greater antiquity than are those of the northeast.

∠A

In view of the relatively narrow interval range of this measure, the monotonous regularity of the curve for ∠A (fig. 11, middle panel) may be somewhat deceptive. Even so, it is apparent that in arc *SW4* (western Great Plains) there is a definite tendency for more abruptly tapered leaves, while in the far southwest the leaves predominantly are more gradually tapered than the normal. We have observed these tendencies previously in the phenocontour maps. Since both extremes occur in hot, arid or semi-arid land, where colonies are relatively small and infrequent, and apparently are not parts of a definite geocline, I conclude that we are observing a rather poor example of genetic drift, in which the influence of natural selection is absent or negligible.

LENGTH AND WIDTH

In the curves for median length and median width (fig. 11, two lower panels), the interaction of genetic drift and selective pressure toward the establishment of microphyllous types, so characteristic of xerophytic vegetation, appears in the southwestern arcs with almost schematic clarity. In general, length is correlated with width; but in the northeastern arcs we see that the two characters may behave independently, the length regularly being considerably greater than in the Ozarks, while the width is generally somewhat less. The various curves presented in fig. 11 appear to testify to the individuality of the genetic mechanisms responsible for all four phenotypes,

and their freedom of action under the pressures of both natural selection and the breeding structure of the populations.

RELATION OF THE CENTRIFUGAL EFFECT IN ∠B TO INTROGRESSION

Having demonstrated the existence of centrifugal modification of the leaf base in genetically more or less "pure" *Asclepias tuberosa interior*, an attempt should be made to apply what we have just learned to the problem of introgression of that subspecies with *A. t. tuberosa*.

In the lower panel of fig. 14, appears a map of the east-central United States from the Ozark plateau to the Atlantic coast. Three features of our previous discussions are superimposed upon this map: the concentric circles of Map VII as they would appear if projected to the east of the boundary of introgression, the horizontal rank of quadrats from *G3* to *G11* of the phenocontour maps (which is chosen because it coincides with the diameter of the concentric circles), and the position of the crests of variability between subspecies *interior*, *tuberosa*, and *Rolfsii* as determined in Map IV. Since the width of the circular areas corresponds to the sides of the quadrats, it is possible to effect a fairly satisfactory comparison of the two sets of data.

In the upper panel of fig. 14, the ordinate is in degrees of ∠B and the abscissa records the positions of the coinciding circles and quadrats as they appear in the map immediately below. The uppermost curve, borrowed from fig. 10, represents the centrifugal modification of ∠B which we might expect to obtain in this region if there were no introgression with the eastern *A. t. tuberosa*. The lower continuous curve represents the actual gradient of the quadrat means, taken from Table III, indicative of the effect of introgression of *A. t. interior* with the eastern subspecies.

If we refer back a moment to the ∠B curves in fig. 7, which were obtained along the horizontal rank of quadrats from *F3* to *F12*, their basic similarity to the quadrats curve in fig. 14 is apparent; in all three curves the influence of the "hump" noted in the circles and arcs gradients may be observed. We shall attempt to provide possible explanations of this feature in paragraphs which will follow, but for the moment it is sufficient to note the participation of the centrifugal effect in introgression of the two subspecies.

Before continuing farther, it is necessary to call attention once again to evidence of the introgression of *A. t. tuberosa* with the Floridian *A. t. Rolfsii*, namely, the abrupt rise of ∠B values at the eastern end of the quadrats curve in fig. 14. It may readily be appreciated that the more or less hastate or cordate leaf base characteristic of the latter subspecies would produce a relatively high ∠B value; and its proximity to the crest of variability between the two subspecies leaves little doubt concerning the change of gradient of which we speak. The Floridian subspecies, in fact, most probably also is concerned in the similar gradient changes

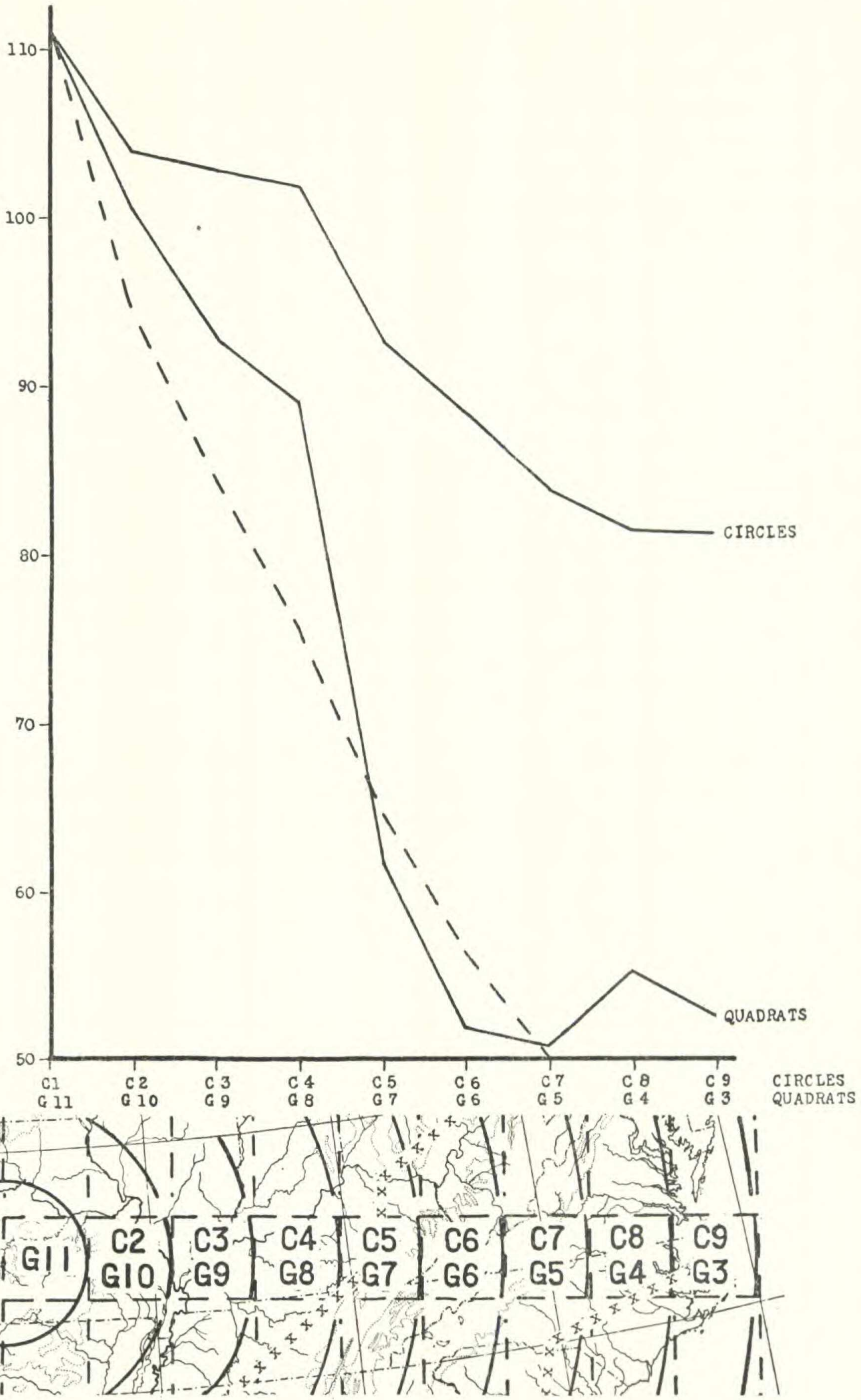


Fig. 14. Comparison of ∠B quadrat means as expected with simple gene diffusion and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa.* Explanation in text.

seen at the eastern end of the ∠B curves in fig. 7. Since our biometric measures have been designed for use only with the other subspecies, the recurrent influence of *Rolfsii* is rather annoying, however instructive.

Hemmed in by *A. t. interior* on the west and northwest, and by *A. t. Rolfsii* on the south and southeast, little remains of *A. t. tuberosa* which may be called genetically pure. Under such conditions, it is impossible to distinguish internal population patterns except upon the lowest level, and very hazardous to speculate concerning the original subspecies parameters. In the absence of any evidence to the contrary, I assume that there is no concentric modification of the leaf base in *A. t. tuberosa* such as we have just demonstrated in *A. t. interior*. Since the quadrat populations upon the Atlantic coast farthest from the probable influence of introgression vary roughly between 47° and 55° with respect to ∠B, I am estimating a leaf base of 50° as a convenient approximation of the characteristic of "pure" *A. t. tuberosa.*

An interesting aspect of the quadrats, or introgression, gradient between subspecies *interior* and *tuberosa* is shown by use of the broken line in fig. 14. This line, purely a hypothesis, is drawn from quadrat *G11* in the central Ozarks to quadrat *G5* in the eastern Appalachians, where the herbarium sample approximates the estimated ∠B parameter of "pure" ssp. *tuberosa.*

The hypothesis of the broken line is that there is a perfectly balanced diffusion of genes between subspecies *interior,* emanating from *G11*, and *tuberosa,* emanating from *G5,* in much the same manner as we might visualize the diffusion of the molecules of two equally miscible inorganic compounds. Since we have good evidence of the centrifugal lowering of ∠B values in *interior,* and are assuming the stability of a value of 50° in *tuberosa,* the broken line is plotted at equally graded intervals between the "circles" curve and the 50° abscissa, to show 100 per cent *interior* and 0 per cent *tuberosa* influence at quadrat *G11*, 0 per cent *interior* and 100 per cent *tuberosa* influence at *G5,* 50 per cent influence of both *interior* and *tuberosa* at *G8,* and so forth, for the intervening quadrats. The points along the broken line, rounded for convenience, as well as the percentage values of the corresponding points along the quadrats curve, are provided in Table XIII.

A comparison of the broken line with the quadrats curve in fig. 14 will show the consistent way in which they differ, for we see that the *interior* influence is greater toward the western half of the cline, and that of *tuberosa* greater toward the eastern half than we would expect if genes were exchanged equally between the two subspecies, other factors being removed. The surplus *interior* influence is seen to increase toward the east, progressively from *G11* to *G8*, whereas that of *tuberosa* would appear to decrease toward the west. Finally, in *G5*, possibly because we have set the estimated parameter of "pure" *tuberosa* too low, the value obtained from the quadrat data appears to show the influence of *Rolfsii.* The latter feature may be neglected as inconsequential for our immediate purpose; but the centrifugal increase of *interior* influence and decrease of *tuberosa* influence is of more interest.

TABLE XIII

COMPARISON OF ∠B QUADRAT PERCENTAGES AND MEANS AS EXPECTED WITH SIMPLE GENE DIFFUSION AND AS ACTUALLY OBTAINED IN THE INTROGRESSION OF *A. T. INTERIOR* AND *A. T. TUBEROSA*

(Explanation in the text)

Quadrat	G11	G10	G9	G8	G7	G6	G5
% *int./tub.* expected	100/0	83/17	67/33	50/50	33/67	17/83	0/100
% *int./tub.* obtained	100/0	94/6	81/19	76/24	27/73	5/95	2/98
$\bar{X}$ expected	111.2	94.6	85.3	75.9	63.7	56.5	50.0
$\bar{X}$ obtained	111.1	100.5	92.9	89.1	61.7	52.0	50.8
d/σ	0.0	3.5	2.1	2.2	0.3	0.8	0.2

Table XIII also presents the quadrat means expected with simple gene flow of the sort we hypothesize, together with the means actually obtained. Finally, the coefficient of abmodality, d/σ, is calculated. A frequent biometric practice is to regard d/σ values >2 as significant and values <2 as probably not significant. If we apply this arbitrary rule to our calculations, we find that the centrifugal increase of *interior* influence probably is significant, while that of *tuberosa* probably is not. The means obtained from the quadrat samples in *G7*, *G6*, and *G5*, therefore, may be regarded as coinciding sufficiently with the hypothesis, and the apparently surplus *tuberosa* influence as dubious.

Several explanations present themselves to account for the interesting properties of the introgression gradient; they are not mutually exclusive nor do they exhaust all possibilities:

1. *Natural Selection.*—In the previous discussion of the centrifugal effect proper, we have seen that the larger number of flowering stems per plant, as well as the increased general vigor, characteristic of the cordate-leaved race of subspecies *interior,* almost certainly would tend to increase the reproductive potential of the plants, and thus might well be of importance in natural selection. Hence, the selective superiority of *interior* might enable it to extend more rapidly and perhaps into a greater variety of habitats than subspecies *tuberosa.* If this explanation is worthy of consideration in connection with the aggressive role of *interior* in introgression with *tuberosa,* it probably is worthy of consideration as a causative agent in the change of gradient ("hump") which we noted originally in fig. 11; *i. e.*, the supersedure of the ancestral race of *interior* with cuneate- or round-based leaves by the younger, cordate-leaved race from the central Ozarks may be due to selective superiority associated with the latter.

2. *Migration Pressure.*—The quadrats gradient of fig. 14 recalls the obvious fact that plants tend to migrate outward from their centers of dispersal through the agency of dissemination and other methods of transport. In this instance, the migratory powers of *interior* may be taken as greater than those of *tuberosa.* Since the seeds of *Asclepias* are classical examples of wind-dissemination, we may construe the direction of the prevailing winds in this section of the United States, from west to east, as favoring this argument.

3. *Dominance.*—The gradient may be indicative of the relative dominance of the *interior* genotype and the recessiveness of that of *tuberosa.* According to Fisher's theory of dominance, I take it that this possible "explanation" is merely a corollary of the first.

4. *Genetic Structure.*—The different degrees of aggressiveness of *interior* and *tuberosa,* on the other hand, may be due to a difference in the structural natures of the respective genotypes which makes the diffusion of the "*interior* influence" somewhat more rapid than that of *tuberosa.* For example, a large gene complex, rather diffuse with respect to loci, might be more easily redistributed in crossing-over than a smaller, more compact one. This suggestion is wholly conjectural and cannot be supported by our present technique, although it deserves theoretic consideration.

If the surplus influence of *interior* which we have just demonstrated with regard to ∠B is due to migration pressure, we would expect to find a similar surplus with regard to ∠A. Accordingly, fig. 15 compares the ∠A quadrat means as expected in simple diffusion of genes and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa.* The method is precisely the same as that employed in the construction of fig. 14, the estimated parameter of "pure" *interior*

TABLE XIV

COMPARISON OF ∠A QUADRAT PERCENTAGES AND MEANS AS EXPECTED IN SIMPLE GENE DIFFUSION AND AS ACTUALLY OBTAINED IN THE INTROGRESSION OF *A. T. INTERIOR* AND *A. T. TUBEROSA*

(Explanation in the text)

Quadrat	G11	G10	G9	G8	G7	G6	G5
% *int./tub.* expected	100/0	83/17	67/33	50/50	33/67	17/83	0/100
% *int./tub.* obtained	96/4	93/7	60/40	46/54	30/70	16/84	4/96
$\bar{X}$ expected	85.5	86.5	87.4	88.2	89.2	90.0	91.0
$\bar{X}$ obtained	85.7	85.9	87.7	88.5	89.4	90.1	91.1
d/σ	0.3	1.3	0.6	0.6	0.2	0.1	0.5

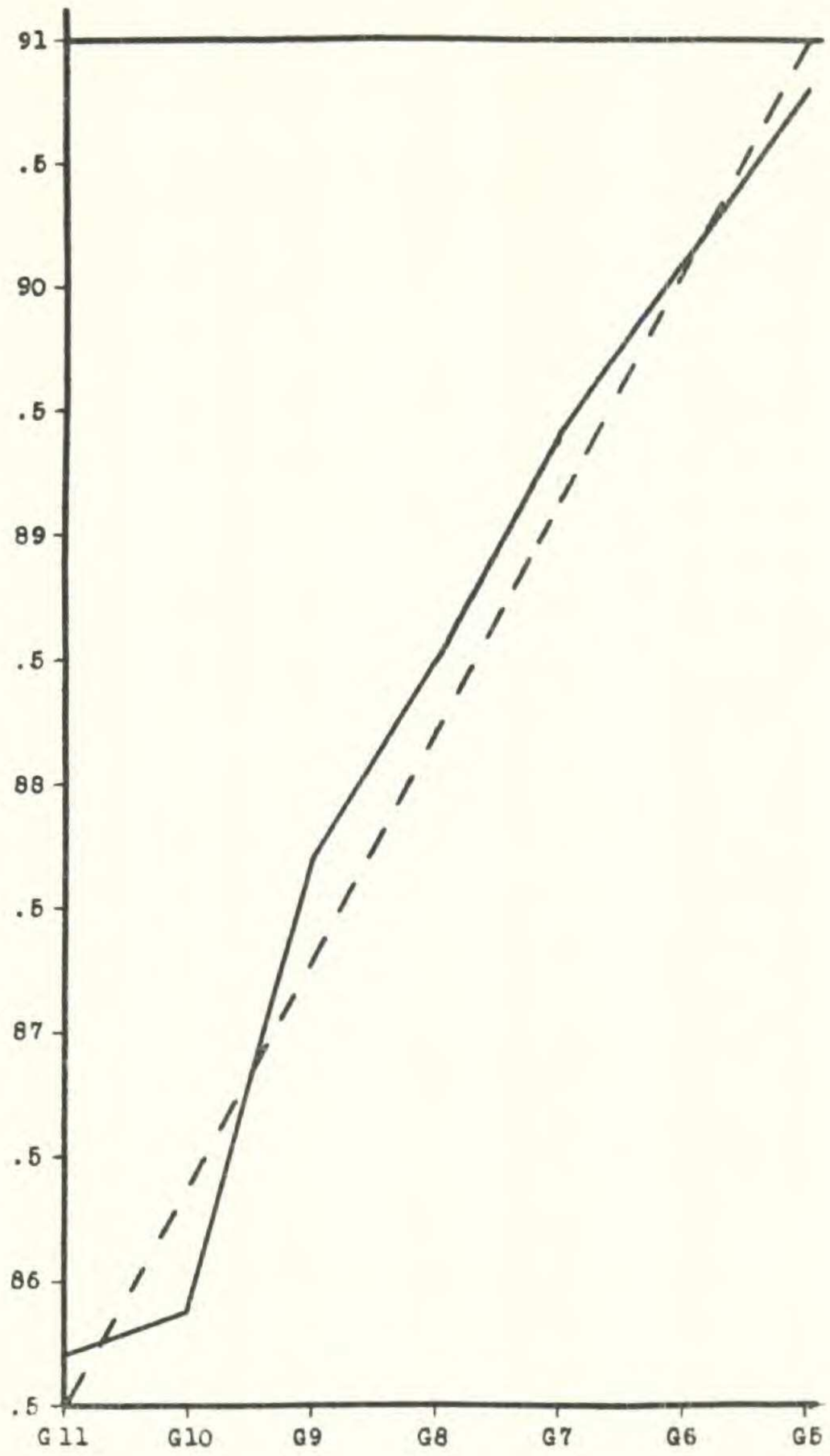


Fig. 15. Comparison of ∠A quadrat means as expected with simple gene diffusion and as actually obtained in the introgression of *A. t. interior* and *A. t. tuberosa*. Explanation in text.

in this case being 85.5° and that of "pure" *tuberosa* 91°. The percentages of "influence" and means, expected and obtained, as well as d/σ values for each quadrat, are provided in Table XIV.

In spite of the fact that the ordinate scale of fig. 15 is made ten times greater than that of fig. 14, to compensate for the correspondingly discrepant range scales of ∠B and ∠A, the close correspondence of the broken line representing the hypothesis and the continuous curve of the actual genocline is apparent. The small d/σ values for each quadrat support the assumption that the genocline, obtained by use of the herbarium specimens, is essentially what one would expect to result from the equal diffusion of genes, and that other factors apparently are of negligible importance in introgression as far as these genotypes are concerned. In fig. 14, then, I believe that we may assume the strong influence of subspecies

interior in the western quadrats to be due to the selective superiority of the cordate-leaved Ozark population. The same factors may likewise be assumed responsible for the concentric modification of ∠B observed within *A. t. interior*.

VII. Discussion and Summary

Asclepias tuberosa, popularly known as "butterflyweed," is a species of herbaceous perennials distributed from Ontario to Sonora, and from Minnesota to Florida. The plants occur chiefly in colonies of from few to over a hundred individuals in a wide variety of habitat from near sea-level to about 6000 feet elevation. They are facultatively self- or cross-fertilized through insect agency, and disperse their comose seed by air currents.

Three subspecies comprise *A. tuberosa: A. t. interior*, centering in the Ozark plateau and extending to southern Ontario, the Rocky Mountains, and northern Mexico, *A. t. tuberosa*, centering in the southern Appalachian Mountains and extending to the Atlantic coast, and *A. t. Rolfsii*, which centers in Florida and extends onto the coastal plain of Alabama, Georgia, and the Carolinas. Since the subspecies apparently are quite panmictic and freely hybridize at the present time, it is assumed that they have had their origin in isolation on the Paleozoic and Early Mesozoic land masses, Ozarkia, Appalachia, and Orange Island, respectively.

The purpose of this study is to investigate the population patterns of the three subspecies, particularly with regard to their apparent introgressive hybridization. This is accomplished by the measurement of leaf characters, which provide the principal systematic criteria of the subspecies. Unfortunately, it is found impracticable to distinguish leaves of all three subspecies by means of a single continuous scale, so only those of *interior* and *tuberosa* actually are measured; information concerning the role of *Rolfsii* is obtained only indirectly in so far as it influences the other data. Measurement of median length and width is in millimeters, and of apical taper (∠A) and shape of base (∠B) in standard degrees of declination, according to a rather elaborate procedure. Leaves are measured from herbarium specimens and from natural colonies growing in the field. The former are considered to yield the best estimate of the natural parameters of the subspecies for various reasons.

From the herbarium data separate phenocontour maps are constructed for ∠A, ∠B, median length, and median width. Isophene systems are plotted to indicate gene flow between subspecies *interior* and *tuberosa* with respect to ∠A and ∠B, the two characters which best differentiate the populations from the systematic standpoint. In the map for ∠B, "crests of variability," indicative of maximum heterozygosity, occur midway of the genocline of *interior* and *tuberosa*, and also about midway between the centers of dispersal of *tuberosa* and *Rolfsii*.

In the maps for length and width, more or less conspicuous increase in leaf size is seen to be associated with the former "crest of variability," and this is interpreted as an indication of hybrid vigor. No heterosis is found to be associated

with the second crest, and neither crest of variability nor heterosis is associated with the genocline of ∠A. It is not practicable to draw isophenes for length and width, but both geoclines and ecoclines are observed, the latter apparently related to restriction of population size under the influence of selection pressure, particularly in the southwest. In all characters, the individual colonies behave as microgeographic races, which are combined variously to form the major population patterns.

One of the most interesting phenomena to be demonstrated is the concentric diffusion from the Ozark plateau of a special modification of ∠B which, because of certain associated selective advantages, appears to be supplanting the ancestral race. A crest of variability is associated with the diffusion of this character, which probably dates since the Pleistocene, but there is no apparent heterosis. For various reasons, it is interpreted as possibly due to a major change of genotype.

The close correspondence of the centrifugal modification of ∠B to Matthew's (1915) hypothesis of the centrifugal migration of primitive organisms is obvious. Although our data confirm the general thesis of Matthew, *viz.*, the peripheral distribution of the supposedly primitive forms, climate clearly is not an active agent in this case.

Analysis of natural populations suggests that ∠A and ∠B are due to multiple factor complexes between which there is slight linkage. Segregation apparently is Mendelian.

Introgression in the subspecies of *A. tuberosa* is believed to proceed from initial hybridization through back-crossing to other heterozygotes and both ancestral types, respectively, to produce a more or less perfect gradation of genotype. Gene flow from either ancestral type is thought to be facilitated by crossing-over to effect redistribution, and the velocity possibly may be dependent upon the distribution of genes, particularly with respect to loci. Velocity of gene flow is observed to be directly proportional to population density. Although gene flow may be equal in either direction, as in ∠A, associated selective advantages of one gene complex may inequalize the balance, as in ∠B. Gene flow may be inequalized also by factors mechanically influencing migration pressure, such as the direction of prevailing winds; this, however, probably is of minor importance in *Asclepias tuberosa*.

The most obvious evolutionary role of introgressive hybridization might appear superficially to be merely the negative one of the obliteration of previous specific or subspecific distinction. However, the resultant increase of potential variability may play an important part in subsequent systematic differentiation.

Introgression of *A. t. interior* and *A. t. tuberosa* appears to proceed more rapidly along roadsides than in undisturbed areas.

During my studies of *Asclepias tuberosa* I have been the grateful recipient of favors from a multitude of friends, unfortunately too numerous to mention individually. These unselfish people, widely distributed throughout this country, enabled me to continue the investigation of geographical variation during the war